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PaleoBios

ISSUES
1 - 28

1967 - 1978

Editors

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PREFACE

The present volume is a collective reprinting of issues 1 - 28 of PaleoBios, published initially during the period 1967 - 1978.

PaleoBios is an outlet for short, occasional contributions of paleontological significance. Since its inception the journal has been managed and edited by graduate students in Paleontology, University of California, Berkeley. We wish to acknowledge the contributions of D.P. Whistler, J.H. Hutchison, L.G. Barnes, D.P. Domning, C.B. Hanson, M.J. Novacek, K.E. Ahern, J. Munthe, S.A. McLeod, A. Berta, and N.J. Harper, editors for the issues in this volume. We wish to extend special thanks to Ralph Gentile of C.J. Graphics and Annemarie Mitchell of the Central Library, U.C. Berkeley. Also, we wish to express our appreciation for the support of the academic and the non-academic staff of the Museum of Paleontology, as well as that of Drs. D.E. Savage, J.T. Gregory, and W.B.N. Berry, Directors of the Museum.

A number of editorial modifications have been made to facilitate the utility of this volume. Typographical errors have been corrected, issue headings have been added to each page, and the page size on issues 1 - 7 has been changed. All plates have been reset for this volume, while figures have been reproduced directly from the original issues. An insert originally included with Issue no. 19 has been reproduced as an appendix to that issue. Finally, a comprehensive index, as well as a table of contents, has been prepared for this retrospective volume.

John J. Chiment
David E. Foster
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PaleoBios

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 1 June 15, 1967

OREODONTS OF THE TICK CANYON FORMATION, SOUTHERN CALIFORNIA

by

David P. Whistler

OREODONTS OF THE TICK CANYON FORMATION, SOUTHERN CALIFORNIA

BY DAVID P. WHISTLER

In 1940, Richard H. Jahns reviewed the stratigraphy of the nonmarine Mint Canyon Formation in the eastern part of the Ventura Basin and separated from it a new formation and fauna. Previous to this work, a controversy existed as to the age of the Mint Canyon Formation, for it contained vertebrates considered indicative of both the Miocene and Pliocene (Kew, 1924, Maxson, 1930, and Stirton, 1933). As a partial solution to this controversy, Jahns demonstrated the presence of an erosional unconformity low in the nonmarine sequence which indicated a shift in source area. He redefined the beds below the unconformity as the Tick Canyon Formation (Jahns, 1940, pp. 163-66).

Additional fossils discovered in the Tick Canyon Formation since Maxson's work, and certain of the forms described by Maxson, comprise the Tick Canyon fauna. Only two specimens described by Maxson are from the Tick Canyon Formation, UCMP 30046, the type of Miolabis californicus and UCMP 23852, a dentary fragment of a Parahippus. Neither of these permitted a definitive age determination. The additional fauna described by Jahns indicates an Arikareean mammalian age (early Miocene), and there is a noteworthy temporal hiatus between the Tick Canyon fauna and the overlying Mint Canyon fauna. In addition, faunas comprising three mammalian ages, late Barstovian, and earlier and late Clarendonian, are now recognized from the Mint Canyon Formation, but this is not the principal concern of this paper.

Several reviews of individual taxa from the Tick Canyon fauna describe either new genera or species (Dawson, 1958, Reeder, 1960). All the described taxa were originally restricted to the Tick Canyon Formation. Unpublished records of these taxa now occur in other California localities.

The composite Tick Canyon fauna as presently known is as follows: a heteromyid rodent, Trogomys rupinimenthae Reeder, 1960, a rabbit, Archaeolagus acaricolus Dawson, 1958, two oreodonts, Merychyus (Merychyus) calaminthus Jahns, 1940, and Merychyus (Merychyus) jahnsi (this paper), a camel, Miolabis californicus Maxson, 1930, and a stenomyline camel (previously unpublished record).

All California Institute of Technology collections are now conserved in the Los Angeles County Museum of Natural History. With the consent of this institution, the author was able to study the entire sample of oreodonts from the Tick Canyon fauna, which includes an additional maxillary fragment collected by Miss Beth Chassé, an associate of the museum.

Jahns (1940, p. 187) specified four specimens as cotypes of the species Merychyus calaminthus; CIT 1383, 1382, 1342, and 1829. Although Jahns implies that all these specimens are from a single quarry sample, CIT 201, the labels on the specimens indicate that CIT 1342 was from another locality within the Tick Canyon Formation, CIT 199. Jahns considered the specimens CIT 1383, 1382, and 1842 adults and the other juvenile. An incomplete skull, CIT 1382, entered significantly into his typification of M. calaminthus. I believe this specimen represents a distinct species and designate it the type of M. (Merychyus) jahnsi, described below.

Schultz and Falkenbach (1947, p. 188) included a discussion of the species M. (M.) calaminthus in their revision of the subfamily Merychyinae, and redefined as a single holotype LACM 1383. They concluded that the incomplete skull, CIT 1382, represented a juvenile individual with dP^4 and M^{1-2}, rather than an adult with M^{1-3}, as reported by Jahns. I agree with Jahns in regarding LACM 1382 as a young adult individual. This is based on several characters. The most anterior cheek tooth present (M^1 according to Jahns, dP^4 according to Schultz and Falkenbach) has well developed roots and the character of the enamel is identical with that of the more posterior cheek teeth. Deciduous dentitions often bear smoother and lighter colored enamel, and this is the case with the juvenile Tick Canyon specimens. Examination of the order of replacement and occlusion in the genus Merychyus, including the juvenile material in the Tick Canyon sample, shows that the dP^4 and M^1 are moderately worn before the M^2 begins to show wear facets. In LACM 1382, the most anterior tooth (M^1, this paper) is moderately worn, but the next tooth (M^2, this paper) displays very little wear. This second tooth should be moderately worn if it is M^1 as inferred by Schultz and Falkenbach. In addition, an unerupted bud of permanent P^4 would be expected to exist below this anterior-most tooth if it is the dP^4. On the contrary, this anterior tooth is strongly rooted and well socketed in the maxillary bone.

Since LACM 1382 represents an adult individual, comparison can be made with the holotype of M. (M.) calaminthus. This comparison reveals several morphological differences and an average size difference of 15 per cent.

Order ARTIODACTYLA
Family Merycoidodontidae
Subfamily Merychyinae
Merychyus (Merychyus) calaminthus Jahns (restricted)

Type: Part of a skull with P^1 to M^3, LACM 1383.
Referred material: Badly crushed fragment of left mandible with P_3 to M_3 inclusive, LACM 1342.
Type locality: CIT 201; west side of small canyon in southwest corner of Section 24, T5N, R15W, San Bernardino Baseline and Meridian, Humphreys Quadrangle (1932), United States Geological Survey (Jahns, 1940, p. 187).
Amended diagnosis: Size slightly smaller (less than two per cent) than M. (Merychyus) crabilli Schultz and Falkenbach; skull apparently with deep antorbital fossa, but prelacrimal vacuity small, if present; malar depth moderate, single large infraorbital foramen above P^4; dentition hypsobrachyodont, superior tooth row straight and closely spaced, superior premolars with fairly complicated patterns, only moderately reduced anterior lophs of P^{3-4}; P^{1-2} set at slight angle to alveolar border; external styles of superior molars moderately prominent.
Discussion: In addition to the above mentioned characters, Jahns noted the presence of a small lingual spur projecting into the fossette in P^4. Schultz and Falkenbach attribute this character to individual variation, however an oreodont skull fragment in the collection of the University of California, Riverside, from an undescribed Arikareean fauna in the Mojave Desert displays this character also. The P_{3-4} in the referred mandible are well worn, but still bear remnants of lingual fossettes, suggesting similar complexity to the upper premolars. Jahns (1940, p. 189-90) also figures

and describes a left pes. This specimen was not definitely associated with any of the skull remains, so it cannot be unquestionably referred to either species.

Merychyus (*Merychyus*) *jahnsi* sp. n. Figure 1

Type: Part of a skull with M^{1-3}; figured as a cotype of *M.* (*Merychyus*) *calaminthus* by Jahns, 1940, plate 2, figure 2 and 3a; LACM 1382. The LM^1 was absent in the original figure but was found in the collection and replaced on the specimen.
Referred material: Nearly complete skull and mandibles of a juvenile, LACM 1829; incomplete skull and mandible of young juvenile, LACM 1384, and juvenile maxillary fragment with C erupting and with dP^{1-4}, LACM 13431.
Locality: Same as for *M.* (*Merychyus*) *calaminthus*.
Etymology: Named in honor of Professor Richard H. Jahns, in recognition of his original work on the Tick Canyon fauna.
Diagnosis: Smallest recognized species of the genus *Merychyus*, a number of measurements averaging 15 per cent smaller than *M.* (*Merychyus*) *crabilli* (Fig. 2); low flat skull, supraoccipital wings widely spread; shallow antorbital fossa, small prelacrimal vacuity with triangular outline; lightly constructed malar; paired infraorbital foramina above P^3, superior molars subhypsodont.
Description: *Skull*: By combining the type and the referred fragment of cranium, LACM 1829, a description of nearly the entire skull is possible.

> Jahns (1940, p. 187): The dorsal surface of the skull, as seen in CIT 1382, is low and flattened, with its highest point at the postorbital constriction. The brain case has a nearly circular horizontal cross section, and its upper surface is marked by two broad, very low temporal ridges. These ridges unite just in back of the glenoid fossae to form a short, narrow sagittal crest that is clearly defined but not prominent. The occipital crests are sharp and well developed.
>
> (p. 188) The malar is of medium build, but the zygomatic arches are light. The elevated orbits are rather small and only slightly elongated

> anteroposteriorly. From the orbits, the lacrimals project forward to occupy a rather extensive area on the face;...The short nasals are widest at their anterior ends. These elements appear to be slightly constricted at the middle, and are rounded posteriorly. The frontals, flat to gently convex, rise to a low ridge at the orbital rim.

There is a shallow, elongate antorbital fossa. The antorbital fossae in *M.* (*M.*) *calaminthus* are not preserved, but a sharp infolding of the lacrimal anterior to the orbit suggests that the fossae were much deeper than in *M.* (*M.*) *jahnsi*. The malar is of somewhat lighter build in *M.* (*M.*) *jahnsi* than in *M.* (*M.*) *calaminthus*.

Schultz and Falkenbach (1947, p. 188) describe the basicranial region, an important area in their distinction of species, as follows:

> ...supraoccipital wings widely spread, possibly less fan-shaped occipital region than in average *Merychyus* examples...

Jahns (1940, p. 188) describes the remainder of the skull as follows:

> In spite of local crushing, several foramina are clearly visible in the basicranial region. A large foramen ovale is situated internally with respect to the glenoid fossa, and a small, round foramen lacerum anterius is completely concealed in ventral view by a marked overhang of the pterygoid. There is no trace of the foramen rotundum, and an alisphenoid canal is not present; instead, the carotid artery appears to have been carried in a short, moderately narrow, but very deep groove. This groove is bounded exteriorly by a stubby pyramidal process situated on the posterior outer edge of the alisphenoid, and interiorly by one of the ventrally diverging pterygoids.
>
> A portion of the rim of the foramen lacerum medium is preserved posterointernally to the foramen lacerum posterius in back of the space occupied by the tympanic bulla.
>
> The infraorbital foramina lie above the middle part of P^3, and the [anterior] palatine foramina occupy positions opposite P^4...

The infraorbital foramen is paired with a smaller foramen lying posterior to and slightly below the principal infraorbital foramen.

No adult mandibles are represented in the sample of this species. The juvenile mandibles, LACM 1829, bear no apophysis below the condyle as is found in the subgenus Metoreodon Schultz and Falkenbach.

Dentition: The type is the only adult available for study, and the specimen bears only the molars. No permanent P^2, P^3, P^4, incisors or inferior canine are available for study. However, P^1 and the superior canine erupt early and are present in two juvenile specimens, LACM 1829 and 1384. These teeth do not differ markedly from those in M. (M.) calaminthus or M. (M.) crabilli. The mandibles of the juvenile LACM 1829 bear early wear M_{1-2} and an unerupted M_3. These teeth seem to be narrower in relation to length than any other described species of the genus Merychyus.

Deciduous dentition: Both referred specimens bear deciduous dentitions which permit a unique opportunity for study of these less commonly described teeth. The dP^4 is molariform and square in outline. It bears a well-developed parastyle, mesostyle, and metastyle. In addition, it appears to bear a small protoconule and hypoconule as low distinct cusps on the labial margins of the fossettes. The posterior loph of the dP^3 is also molariform, except that it lacks the styles. There is also a small hypoconule on the labial margin of the fossette in this tooth. The anterior loph is somewhat reduced, but bears two shallow, anteriorly opening fossettes. The dP^2 is two-lophed, as long as the dP^3, but only as broad as the anterior loph of the latter. The labial surface bears no styles, and any fossettes that may have been present are completely worn away.

The dP_2 and dP_3 do not differ markedly from the permanent P_2 and P_3 in M. (M.) crabilli, except for smaller size. The dP_4 is three-lophed with an increase in loph size from the anterior to the posterior loph. There is no lingual cingulum, but weakly developed labial cingula are present at the base of the crown between the lophs.

Figure 2 is a ratio diagram of selected characters in the skull and superior and inferior dentitions of M. (Merychyus) crabilli, M. (Merychyus) minimus Schultz and Falkenbach, M. (Merychyus) calaminthus, and M. (Merychyus)

no. 1

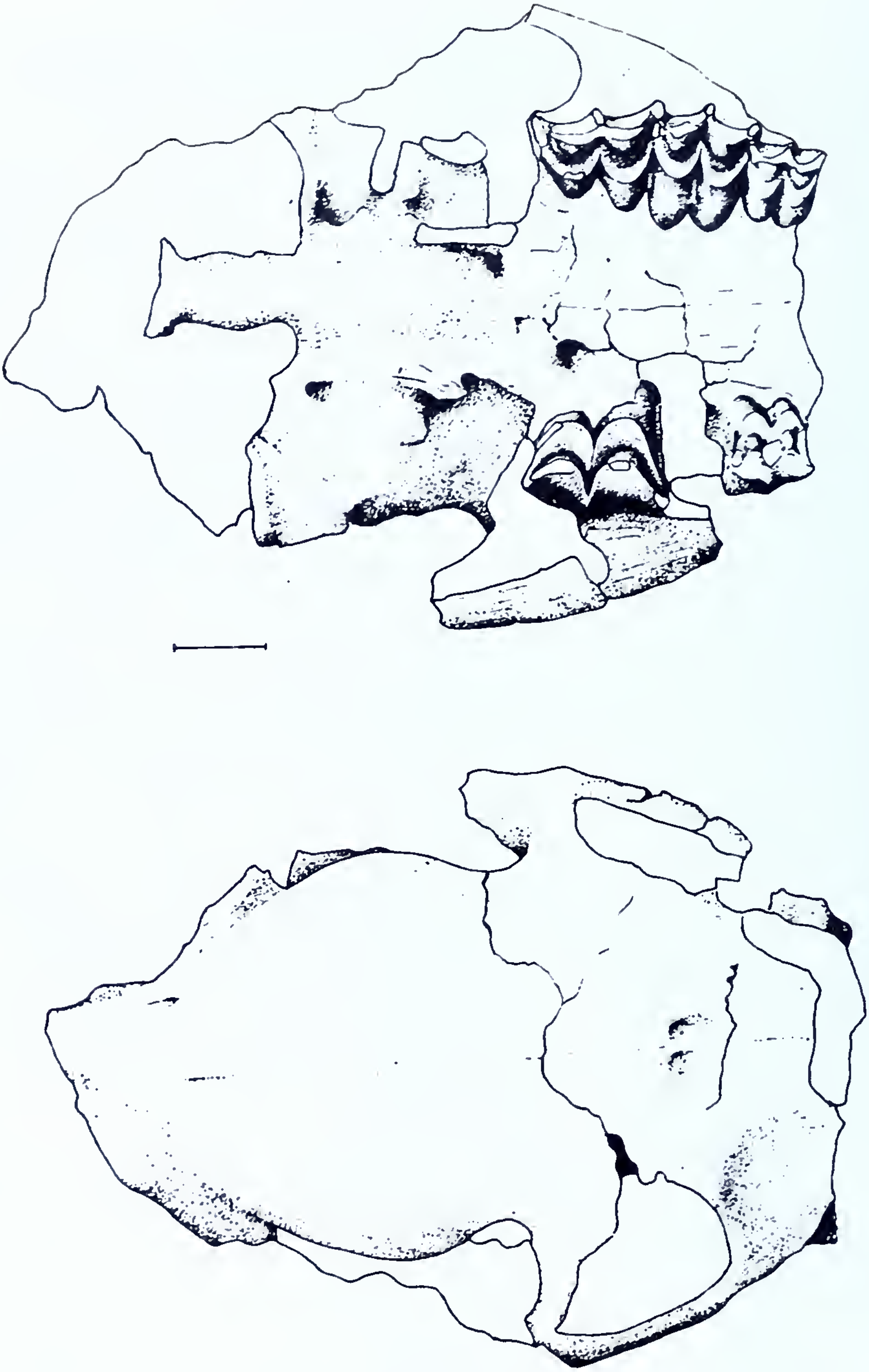

Figure 1 - *Merychyus* (*Merychyus*) *jahnsi* sp. n., holotype, LACM 1382, palatal view showing right $M^{\underline{1-3}}$ and left $M^{\underline{1}}$ and $M^{\underline{3}}$, and dorsal view. Scale equals 1 centimeter.

jahnsi. This method for graphical representation of size differences is taken from G. G. Simpson (1941) which includes a complete explanation of the construction and interpretation of this figure. The method essentially compares the relative proportions of dimensions in any number of different species (three in this case) to a single form arbitrarily picked as the standard of comparison, *M.* (*Merychyus*) *crabilli* in this case. The dimensions are converted to a geometric or logarithmic scale in order that an absolute ratio of numbers will be represented by the same distance plotted on the graph. Since we desire to ignore absolute values and represent only ratios, the differences between logarithms are plotted. The log difference scale is plotted on the ordinate and the various dimensions on the abscissa. Negative log difference values represent a ratio which is less than one, or in other words, a ratio in which the standard of comparison is larger than the form to which it is being compared. The horizontal lines plotted along the ordinate at each character are a log measure of the estimated range of that character. This estimate was obtained by taking 3.24 times the standard deviation (see Simpson, *et al.*, 1960). The small number indicates the sample size. Figure 2 reveals that *M.* (*M.*) *jahnsi* is consistently smaller than *M.* (*M.*) *crabilli*, well outside of the estimated maximum variability found in the latter. However, at least in relation to the proportion of the characters compared, *M.* (*M.*) *jahnsi* displays a close resemblance to *M.* (*M.*) *calaminthus*. The presence of long shallow antorbital fossae, paired infraorbital foramina, a relatively shallower malar and a relatively smaller M^1 serves to distinguish further *M.* (*M.*) *jahnsi* from *M.* (*M.*) *calaminthus*.

PHYLOGENETIC POSITION OF THE TICK CANYON OREODONTS

There are a number of unpublished oreodont records from Southern California which yield pertinent information about the phylogenetic position of the Tick Canyon oreodonts. The Hemingfordian Boron fauna (Whistler, University of California, Riverside, Master's thesis, 1964) contains two well represented species of *Merychyus* which display affinities with *M.* (*M.*) *calaminthus* and *M.* (*M.*) *jahnsi*. Both an unpublished Arikareean fauna in the Mojave Desert and the Hemingfordian

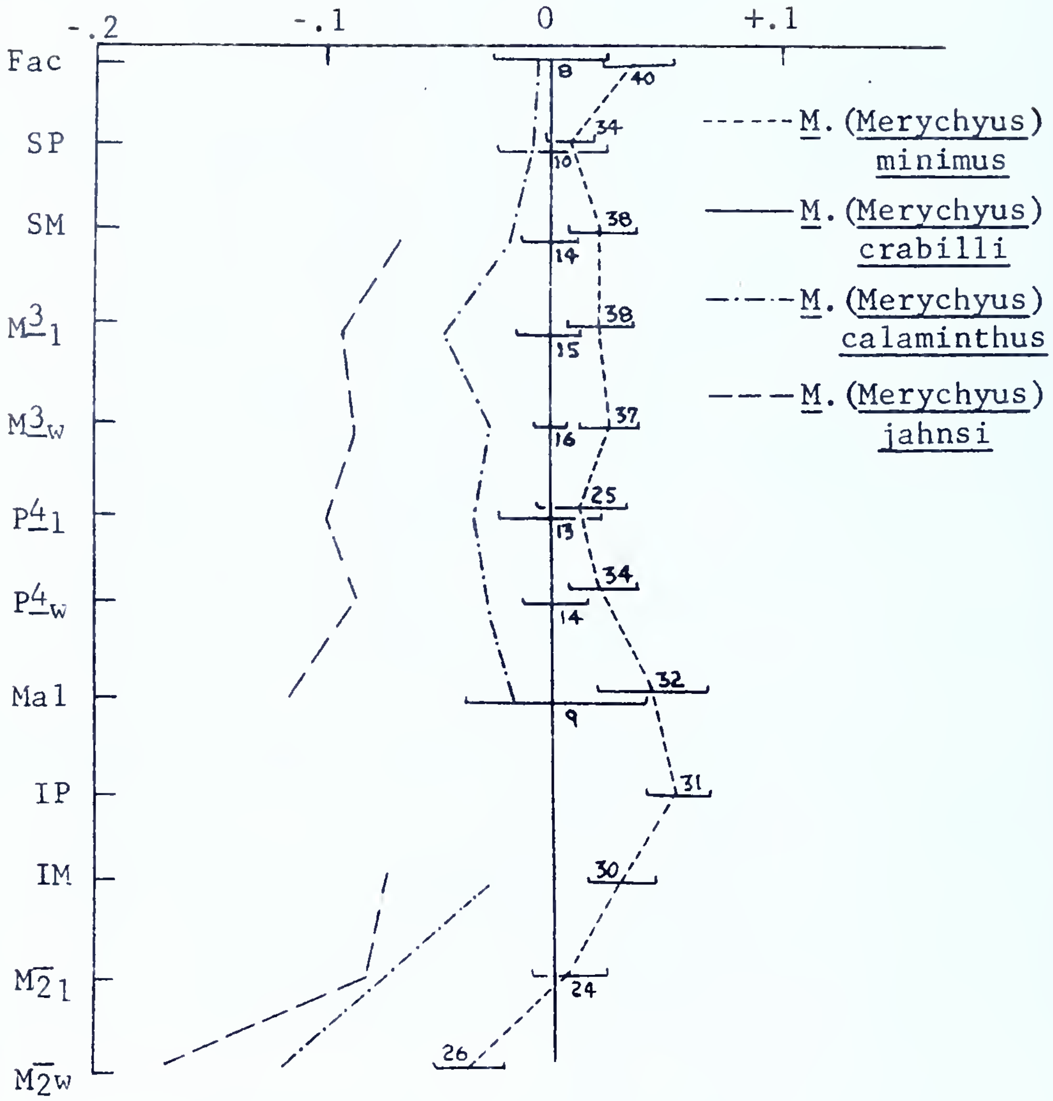

Figure 2 - Ratio diagram of various skull dimensions in M. (Merychyus) calaminthus, M. (M.) jahnsi, M. (M.) crabilli and M. (M.) minimus. Fac-distance from anterior base of canine to anterior rim of orbit; SP-length of superior premolar series; SM-length superior molar series; $M^3{}_1$-length M^3; $M^3{}_w$-width anterior loph M^3; $P^4{}_1$-length P^4; $P^4{}_w$-width P^4; Mal-malar depth; IP-length anterior premolar series; IM-length inferior molar series; M_{2_1}-length M_2; M_{2_w}-width anterior loph M_2. For explanation of graph, see page 6 or Simpson (1941). Data for M. (M.) crabilli and M. (M.) minimus taken from Bader (1955).

Phillips Ranch fauna (Buwalda and Lewis, 1955) contain similar oreodont species.

Therefore, two local lineages appear to be present in the Mojave Desert region. One of these lineages, *M.* (*M.*) *calaminthus*, and similar or large species, displays very little change except for an increase in size and appears to die out in the Hemingfordian.

The other lineage is best represented by the species of *Merychyus* at Boron which was referred to the subgenus *Metoreodon*. This Boron form has a shallow antorbital fossa and paired infraorbital foramina, both of which are developed in *M.* (*M.*) *jahnsi*. A specimen from the Mojave Arikareean site also bears paired infraorbital foramina. *Merychyus* (*Metoreodon*) *relictis* *fletcheri* Schultz and Falkenbach, a much larger and only questionably related form, occurs low in the Barstow Formation. The Barstow record is the last occurrence of the subfamily Merychyinae in Southern California.

It is premature to say with certainty, but it appears that there may be one or more endemic lineages of merychyine oreodonts evolving in the Mojave Desert region during the Miocene.

I would like to thank Mr. Karoly Fogassy who prepared the illustrations and Richard H. Tedford who supplied financial assistance and critical discussion of the manuscript.

TABLE 1

Comparative measurements in the skull of *Merychyus* (*Merychyus*) *calaminthus* and *M.* (*Merychyus*) *jahnsi*. All measurements in centimeters.

	M. (*M.*) *calaminthus*		*M.* (*M.*) *jahnsi*	
	LACM 1383	LACM 1382	LACM 1829	LACM 1384
Facial length, C to anterior rim of orbit	58*		37.0	28.0
Malar depth below orbit	13.2	10.0	9.2	
Palate width at M^1	21.3	16.1	19.0	14.4
Length P^1-P^4	28.0			
Length M^1-M^3	36.0	30.6	31*	
Length C-M^3	78*		55*	
Length P^4	7.0			
Width P^4	9.1			
Crown height P^4	10.0			
Length M^3	15.5	13.6		
Width M^3	11.8	12.0		
Crown height at mesostyle M^3	11.0	12*		
Crown height at mesostyle M^1	5.0	2.8	6.0	
Crown height at mesostyle M^2	8.7	8.0	9.0	5.9
Length dP^2-dP^4			17.8	
Length dP^2			5.5	
Length dP^3			6.7	
Length dP^4			7.2	

* Estimated measurement

nc. 1

TABLE 2

Comparative list of measurements in the mandible of *Merychyus* (*Merychyus*) *calaminthus* and *M.* (*Merychyus*) *jahnsi*. All measurements in centimeters.

	M. (*M.*) *calaminthus*	*M.* (*M.*) *jahnsi*	
	LACM 1342	LACM 1829	LACM 1384
Mandible depth below P_2		11*	14.1
Length of symphysis			18.1
Length M_1-M_3	35.8	31*	
Length C-M_3		56*	
Length M_2	10.0	11.1	11.4
Width anterior loph M_2	7.4	6.7	
Crown height, anterior loph M_2	3.1	1*	
Crown height, anterior loph M_1	2*	5*	6.8
Crown height, anterior loph M_3	8.0		
Length dP_2-dP_4			23.0
Length dP_2			6.2
Length dP_3		6.0	6.8
Length dP_4		11.1	11.2

* Estimated measurements

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PALEOBIOS

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Museum of Paleontology, Berkeley

No. 2 July 15, 1967

PRE-BURIAL ABRASION OF ARTICULATED ASTEROID SKELETONS

by

D. Bryan Blake

PRE-BURIAL ABRASION OF ARTICULATED ASTEROID SKELETONS

BY D. BRYAN BLAKE

Abstract

Although asteroids usually become disarticulated rapidly after death, Recent forms collected on the beach of Baja California show noteworthy transport abrasion but little tendency for disarticulation. A relatively complete fossil starfish therefore cannot be, by itself, considered proof of rapid deposition of the containing sediment; in evaluating ossicle morphology of such specimens, the possibility of pre-depositional abrasion should be considered.

The individual ossicles of an asteroid skeleton are not sutured to one another but are bound together by muscle and dermal tissue. Unless an asteroid is quickly buried upon death, the tissues usually decompose and the skeleton disarticulates. Therefore, discrete ossicles or fragments are more common as fossils than entire tests. Most discrete fossil ossicles are abraded evenly on all surfaces indicating that this wear usually occurs after disarticulation. The observations recorded here indicate that this is not always the sequence of events.

Complete fossil starfish are rarely discovered and generally have been considered indicative of rapid burial. However, a small sample of dead Recent asteroids collected on the beach on Cerralvo Island, near La Paz, Baja California shows that, at least under certain conditions, the dermal tissue may be resistant to decomposition and permit transportation and abrasion of the skeleton prior to burial. This sample contains the following species:

no. 2

Nidorellia armata (Gray) (3 specimens)
Pentaceraster cumingi (Gray) (5 specimens)
Pharia pyramidata (Gray) (2 specimens)
Phataria unifascialis (Gray) (3 specimens)
Asteropsis carinifera (Lamarck) (1 specimen)

The actinal surfaces of the arms and the inframarginal ossicles of the disc are highly abraded on all specimens of *Pentaceraster* (Fig. 1a-d). There is no surface ornamentation remaining on the ossicles near the arm tip and little on those in the interbrachial position. The basic outline of these ossicles has been changed. The minor amount of differential weathering between the marginal ossicles and the enclosing dermis illustrates the resistant nature of this tissue and its physical resistance to abrasion. The oral surfaces of the discs are arched and were not in contact with the substrate. Most granules and pedicellaria remain on the oral intermediate ossicles. The spines are present in the ambulacral furrows nearly to the arm tip, protected by the relatively prominent oral intermediate and inframarginal ossicles. The abactinal surface is somewhat abraded; the most prominent spines and projecting portions of the ossicles are lost, while the fine granules of the sides of the ossicles and the papular area remain intact. The arm tips of several specimens are in the process of breaking away, perhaps by shrinkage and breakage of the dermis during desiccation.

The specimens of *Nidorellia* are similar to *Pentaceraster* in the abrasion suffered. However, one specimen is more worn on the oral surface, another on the aboral surface indicating that this flat form may be unstable in the surf regardless of the surface toward the substrate.

In contrast to *Pentaceraster* and *Nidorellia*, which have heavy tests, those of *Phataria* and *Pharia* are light. The surficial tissue has been largely removed in specimens of these genera, but the individual ossicles show only moderate wear.

In life, the plates of *Asteropsis* are covered by a thick fleshy tissue. In the specimen of this genus in the collection, the fleshy layer has served to protect most ossicles but projecting spines have been abraded.

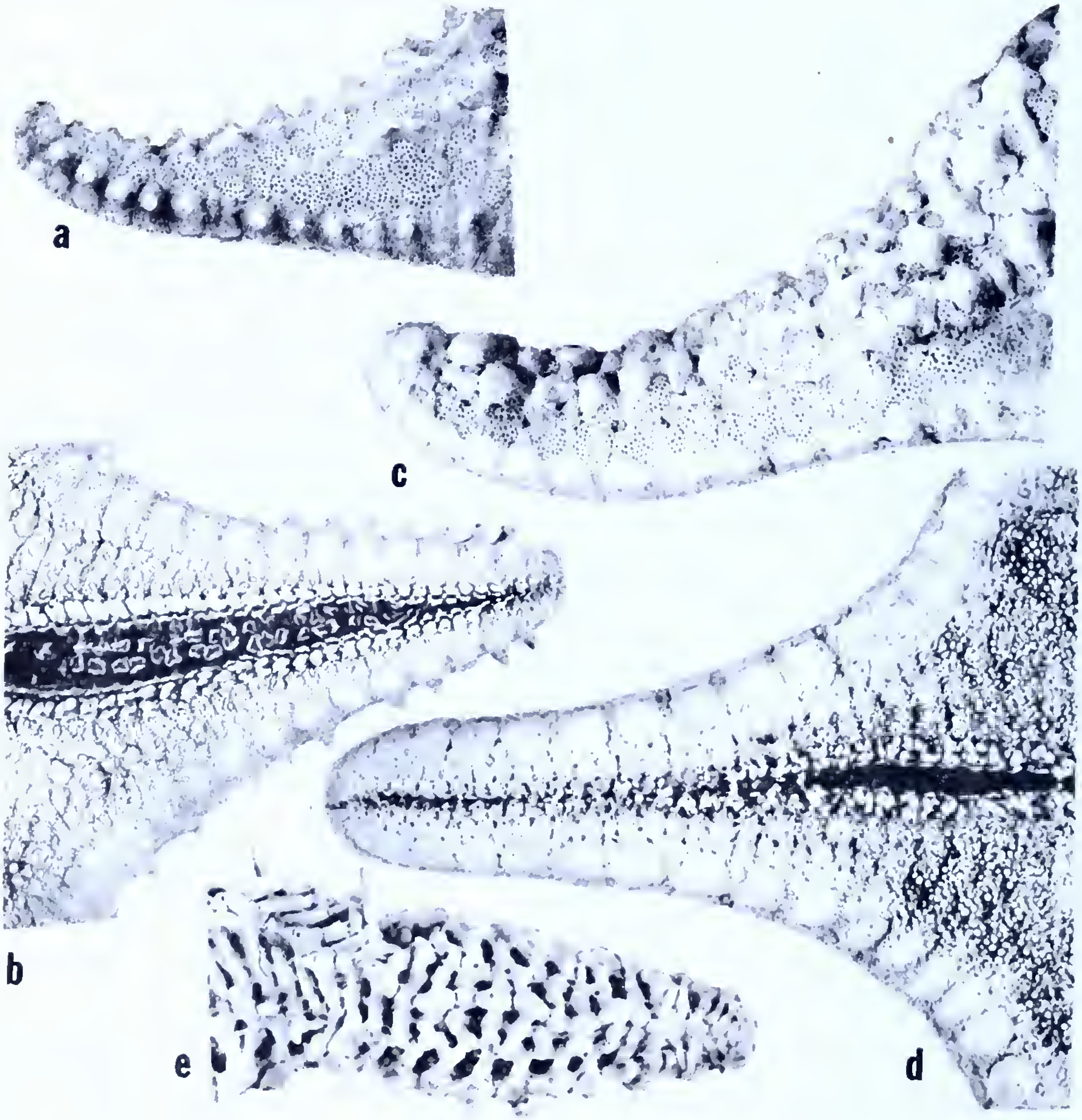

Figure 1 - a-d, Pentaceraster cumingi. a-b, UCMP 30290, lateral and oral views of abraded arm. c-d, UCMP 35087, lateral and oral views of unabraded arm. e, Asteropsis carinifera, UCMP 12106, aboral view of arm. Natural size.

In another specimen of *Asteropsis*, collected from the west coast of Baja California, the soft tissues have been almost entirely lost, yet the skeleton remains articulated (Fig. 1e). There is no evidence of physical abrasion on this specimen.

Steinbeck and Ricketts (1941) report *Pentaceraster* from between 3 and 40 fathoms, and *Nidorellia*, *Pharia*, and *Phataria* from the intertidal zone. Sladen (1889) reports *Asteropsis* from shallow water. Therefore, all the present species are from shallow water or are intertidal; none need have been transported far prior to arrival on the beach. The climate of the area is arid, and certainly contributed to the preservation once the specimens were washed up on the beach. The considerable wear of the ossicles shows that the specimens were transported and abraded by surf action, however. They were in water, wet, and presumably subject to bacterial decomposition, yet the dermis had not yet decomposed and the ossicles had not disarticulated.

These observations indicate that a relatively complete fossil starfish is not necessarily proof of rapid deposition of the entombing sediment; the test must be examined for evidences of pre-depositional transportation. Further, in evaluating any smooth surface of the ossicles of a fossil starfish, the possibility of transportation and abrasion prior to disarticulation must be considered.

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PALEOBIOS, No. 2, 1967.

PALEOBIOS

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 3

July 15, 1967

A PLEISTOCENE VAMPIRE BAT (Desmodus stocki) FROM POTTER CREEK CAVE, SHASTA COUNTY, CALIFORNIA

by
J. Howard Hutchison

A PLEISTOCENE VAMPIRE BAT (Desmodus stocki) FROM POTTER CREEK CAVE, SHASTA COUNTY, CALIFORNIA

BY J. HOWARD HUTCHISON

The range of Recent and previously known fossil vampire bats, Desmodontidae, does not extend farther north than 30° north latitude or farther west than 113° west longitude (Hall and Kelson, 1959). The discovery of Desmodus limb bones in the original 1902 and 1903 collections of W. J. Sinclair and E. L. Furlong from Potter Creek Cave, Shasta County, California, thus considerably extends the range of the genus to the north and west (Fig. 1). The Potter Creek Cave site, University of California Museum of Paleontology locality 1055, is at an elevation of 1500 ft., 40° 47' 02" north and 122° 16' 51" west, and presently within the Transition life zone. Although several extinct late Pleistocene (Rancholabrean) taxa are reported from this site by Sinclair (1904, 1905), Miller (1911), and Stock (1918), most of the non-extinct fauna still lives in the area.

The Desmodus material, UCMP 4017 (Fig. 2), from Potter Creek Cave consists of seven humeri, most are partly damaged. Although the means of the measurements of the humeri (Table 1) from Potter Creek Cave average slightly greater than those from other Pleistocene localities, I could detect no morphological differences among the various Pleistocene forms.

Two extinct species of Desmodus have been described from the late Pleistocene deposits of North America: D. stocki Jones (1958) from Nuevo León, Mexico, and D. magnus Gut (1959) from central Florida. Both species are larger than the only living species of D. rotundus (Geoffroy St. Hilaire). The description of D. magnus was submitted only eleven days after that of D. stocki and neither author was apparently aware of the other's work. Olsen (1960) attempted to distinguish D. magnus from D. stocki on additional material of the former, but he did not compare his material with actual specimens of *D. stocki*. He assumed that *D. stocki* resembled *D. rotundus* in the skull features. Thus, the distinctiveness of *D. magnus* cannot be considered as demonstrated.

Comparison of the type skull of *D. stocki*, Los Angeles County Museum No. 2129, with Olsen's description and figures of the skull of *D. magnus* indicate the following similarities. The glenoid fossae are relatively as large, and the step or swelling at the point of fusion between the basisphenoid and basioccipital is as great. The foramen hypoglossi are equally well pronounced. I had difficulty in determining the "decided ventral deflection" of the paroccipital process in the specimen of *D. rotundus* that I examined. The differences between the living and fossil forms seem rather subjective and are not apparent in Olsen's figures

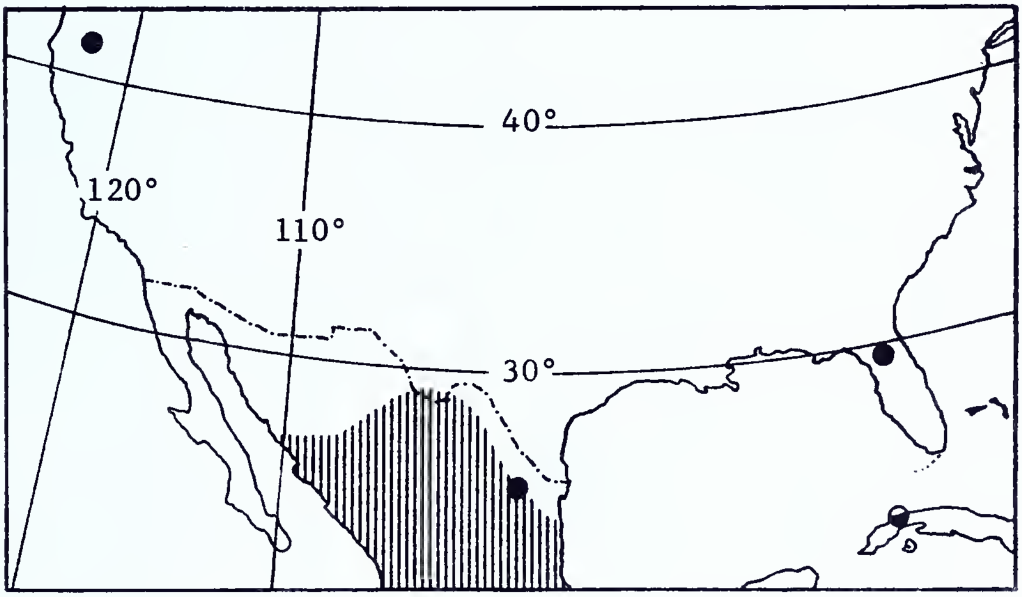

Figure 1 - Distribution of fossil and Recent *Desmodus* in North America. Shaded area indicates the geographic range of Recent *D. rotundus*; closed circles indicate *D. stocki* localities; the half closed circle indicates locality of extinct Cuban *D. rotundus* population.

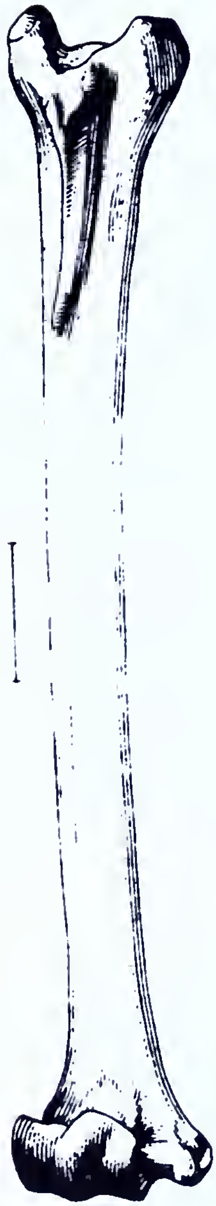

Figure 2 - Desmodus stocki, UCMP 4017, right humerus with small areas of the deltoid crest restored from other specimens. Anterior view. Potter Creek Cave, Shasta County, California. Scale equals five millimeters.

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TABLE 1

Measurements of the humeri of *Desmodus stocki* in millimeters.

Measurement	California Potter Creek Cave			Nuevo León San Josecito Cave			Florida Reddick		
	Mean	(Range)	No.	Mean	(Range)	No.	Mean	(Range)	No.
Length	43.8*		1	43.63	(39.3-47.5)	42	41.14	(38.5-53.5)	21
Proximal width	6.77	(6.75, 6.8)	2	6.27	(5.8-6.8)	47	6.43	(6.1-6.9)	46
Distal width	6.95	(6.5-7.1)	5	6.78	(6.4-7.3)	52	6.69	(6.3-7.3)	66
Medial width	2.67	(2.5-2.8)	7	2.52	(2.0-2.9)	56	2.67	(2.4-2.9)	49

*Two other specimens were damaged but both were over 42.0 mm. as preserved.

of D. magnus. The mastoid and paroccipital processes of the D. stocki specimen are damaged and thus not comparable.

Considering the known similarities between the fossil forms, there seems little reason to retain D. magnus as distinct from D. stocki. The known Pleistocene continental forms may thus be considered as single species on the basis of size and a few skull features. The Potter Creek Cave Desmodus is referred to D. stocki on the basis of size.

Some confusion has arisen in the literature as to the exact localities of specimens of the Florida Desmodus. Brodkorb (1959) listed Desmodus, n. sp., from Arredondo and referred to Gut, in press at that time. Gut (1959) in describing the new species, D. magnus, designated as the holotype a specimen from Reddick and referred a humerus from Haile to the new species. Gut made no mention of any specimens from Arredondo. Olsen (1960) stated: "However, the Florida vampire, Desmodus magnus, is known only from a Pleistocene cave in Marion County near Reddick, Florida (Gut, 1959). Although well known Pleistocene deposits are present in Sabertooth Cave, a few miles to the south and Haile and Arredondo, a few miles to the north, none of these localities has yielded up a single bone collected from these sites." This statement is, in part, in direct contradiction to previous reports. In examining collections from Arredondo II and Haile XIB, I found additional material of Desmodus. This material as well as additional material donated by Gut from both Reddick and Arredondo is preserved in the collections of the Florida State Museum in Gainesville. Desmodus stocki thus seems to be of common occurrence in the late Pleistocene cave and fissure deposits of Florida and more widely distributed in North America than previously suspected.

I wish to thank Dr. J. R. Macdonald for the loan of the type specimen and limb bones of Desmodus stocki, and R. Wolff for photographic assistance. Figure 1 is by Mr. Owen J. Poe.

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PALEOBIOS

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 4 February 1, 1968

Megabelodon minor (MAMMALIA, PROBOSCIDIA), A NEW SPECIES OF MASTODONT FROM THE ESMERALDA FORMATION OF NEVADA

by
J. E. Mawby

no. 4

MEGABELODON _MINOR_ (MAMMALIA, PROBOSCIDEA), A NEW SPECIES OF MASTODONT FROM THE ESMERALDA FORMATION OF NEVADA*

J. E. Mawby

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*A contribution from the University of California Museum of Paleontology.

ABSTRACT

A single fossil mandible from the Esmeralda Formation (Late Miocene-Early Pliocene) of Nevada represents a new species of gomphotheriid proboscidean, allied with the "spoon-billed" mastodonts of the Tertiary of the Great Plains. Mandibles with long symphysis but no lower tusks were developed in at least three independent lines of Tertiary gomphotheres, represented by the genera *Megabelodon*, *Gnathabelodon*, and *Eubelodon*.

INTRODUCTION

In September, 1961, during a study of the Clarendonian vertebrate faunas and the stratigraphy of the Esmeralda Formation in the area around Cedar Mountain in western Nevada, I collected a mandible of a small gomphotheriid, showing affinities with the "spoon-billed" mastodonts of the Miocene and Pliocene of the Great Plains area. The Cedar Mountain discovery is apparently the first record of this specialized group of proboscideans in the Great Basin.

Specimen and locality numbers are those of the University of California Museum of Paleontology, Berkeley, California. All measurements are in millimeters.

Order PROBOSCIDEA
Family Gomphotheriidae
Megabelodon minor, n. sp.

Type: UCMP 67101, mandible with right M_3, parts of right M_2, left M_1, left M_3.
Locality: UCMP loc. V-6145, Gomphothere locality. Mineral County, Nevada. On the north flank of the Cedar Mountains, three miles west of Warrior Mine. Latitude 38° 36' 54" N; longitude 117° 52' 18" W.
Age: Late Barstovian or early Clarendonian (Late Miocene or Early Pliocene). Unfortunately, it is not possible to specify the age of this specimen more exactly. The Esmeralda Formation in the area around Cedar Mountain

contains both Barstovian and Clarendonian faunas. The mandible here described was an isolated find, in an area separated by block faulting from localities of known age. The strata at locality V-6145 are geographically close and lithologically similar to a sequence of beds containing a molluscan assemblage similar to those which elsewhere in the Cedar Mountain area are associated with late Barstovian mammals (Firby, 1963, 1966).

Diagnosis: Small longirostrine gomphotheriid, lacking lower incisor tusks; symphysis less elongate than in other species of Megabelodon, broadened and flattened distally; lower molars relatively narrow, highcrowned; M_3 with four lophids and simple talonid.

Description:

M_1: The first molar is represented only by a worn-out remnant from the left side. The right M_1 was lost before burial, and may have been shed before death.

M_2: Enough fragments of the right M_2 were recovered to make possible the reconstruction of most of the base of the tooth and the posterior half of the crown. The tooth was well worn. The crown consisted of three lophids, with simple ectotrefoils on at least the second and third lophids (Fig. 1).

M_3: The right M_3 is preserved in the jaw, where it was just coming into function. There is a very small wear facet on the tip of the first lophid. The posterior part of the left M_3 was also recovered. M_3 has four lophids and a simple talonid. Anterior and posterior spurs on the labial (pretrite) hemilophids would form simple ectotrefoils with wear. The trefoil spurs are bluntly serrate, especially on the first lophid. There are no central conules in the valleys. The lingual (posttrite) hemilophid of the first lophid appears twisted, so that its labial moiety lies nearly anterior to the lingual moiety. The junction of the two hemilophids is therefore near the anterior side of the lophid. There is an anterior spur or accessory column on the lingual hemilophid of the third lophid. The tooth is relatively highcrowned (Fig. 2).

Mandible: The outstanding character of the mandible is the tuskless, scoop-like symphysis. Although the dorsal and lateral surfaces of the symphysis are poorly preserved, the body of the symphysis is nearly complete. There is no trace of incisor alveoli, and it is clear that no tusks were present. The amount of deflection of the symphysis is obscured by fracturing, but it must have been moderate--probably 15° or less. The deep, asymmetrical lingual groove is bounded by heavy ridges, reaching nearly to the tip of the symphysis. The bone of the extreme tip is too poorly preserved to show clearly whether there was a thickening or rugosity at the tip as in Megabelodon lulli (Osborn, 1936, fig. 666), but this may have been the case. In addition to two mental foramina on the ramus below the anterior end of M_1, there appear to have been at least two foramina along the symphysis, rather than one large foramen as in some advanced longirostrine gomphotheres. The horizontal rami are relatively slender (Fig. 1).

Discussion: Three genera of longirostrine gomphotheriids are characterized in part by the absence of lower incisor tusks: Gnathabelodon Barbour and Sternberg, 1935; Eubelodon Barbour, 1914; and Megabelodon Barbour, 1914.

Gnathabelodon thornei Barbour and Sternberg, from the Pliocene of Kansas, is distinguished by the extreme enlargement of the flaring, shoehorn-like symphysis, and by the short, broad M_3 (Osborn, 1936, pp. 711-714).

Eubelodon morrilli Barbour, from Devil's Gulch, Brown County, Nebraska, is distinguished by its narrow, tapering symphysis, and by the complex, doubly trefoiled molars. (op. cit. pp. 601-611).

Megabelodon Barbour was originally described as a subgenus of Tetrabelodon (=Gomphotherium), and later raised to generic rank. The type species is M. lulli (Barbour), from Cherry County, Nebraska. Osborn's treatment of the group varies, but in his "Final Classification" (1936, p. 738), he lists Megabelodon as a distinct genus, in which he includes M. lulli, M. joraki (Frick) and M. cruziensis (Frick), both from the Santa Fe beds of New Mexico, and M. phippsi (Cook) from Ainsworth, Nebraska. Osborn elsewhere suggests (p. 324) that the two Santa Fe species are probably synonymous, that both may be synonyms of M. phippsi, or (p. 326) that M. joraki may be a synonym of M. lulli.

Megabelodon lulli is a large and extremely long-jawed species. Barbour (1914, plates 3-6) originally restored the mandible with a pair of slender tusks. Additional material, collected later, demonstrated that the symphysis lacked tusks, but had an expanded, rugose tip (Osborn, 1936, pp. 707-709). The molar teeth of the type mandible are too worn for comparison, but Osborn, (ibid.) mentions "very simple and only four crested" molars in a referred mandible.

Megabelodon phippsi seems to be similar to M. lulli, but apparently differs in the complexity of the molars. M_3 has four lophids, as in M. lulli, but Cook (1928, p. 40) speaks of "small double trefoils on both meta- and trilophids,...[and] on the tetartolophid."

The position of M. joraki and M. cruziensis is uncertain. The molars of the type of M. joraki are too worn for comparison, but the M_3 of M. cruziensis has five lophids. Osborn (1936, p. 324) states that there are "partly closed" incisor alveoli in the mandibles of both M. cruziensis and M. joraki. The skull of M. cruziensis also lacks tusks and apparently has partly closed incisor alveoli (Frick, 1933, fig. 10). Osborn suggests that the absence of tusks in these specimens may have been a sexual character. It seems to me more likely to have been a pathologic condition. In either case, it appears unlikely that these forms should be referred to Megabelodon.

Megabelodon minor is much smaller than any of the previously described species of Megabelodon (Table 1). In fact, the tooth dimensions of M. minor place it among the smallest of the post-Oligocene proboscideans recorded. A few of the lower third molars of European Gomphotherium angustidens are as short, though wider (Lehmann, 1950, pp. 179, 185) and the teeth from the Burdigalian of Portugal, described as Trilophodon slisiponense by Zbyszewski (1949, p. 57), are smaller (125 x 55, 115 x 55). The symphysis of M. minor is relatively and actually much shorter than those of other Megabelodon specimens. In M. lulli and M. phippsi, the symphysis is more sharply down-turned than in M. minor. Available information on the molar teeth of Megabelodon lulli and M. phippsi is inadequate for detailed comparisons with M. minor. M_3 is four-lophed in all three species. In M. phippsi, the pattern of M_3 is evidently more advanced in the development of secondary trefoils. Megabelodon minor is readily distinguishable from all other species of

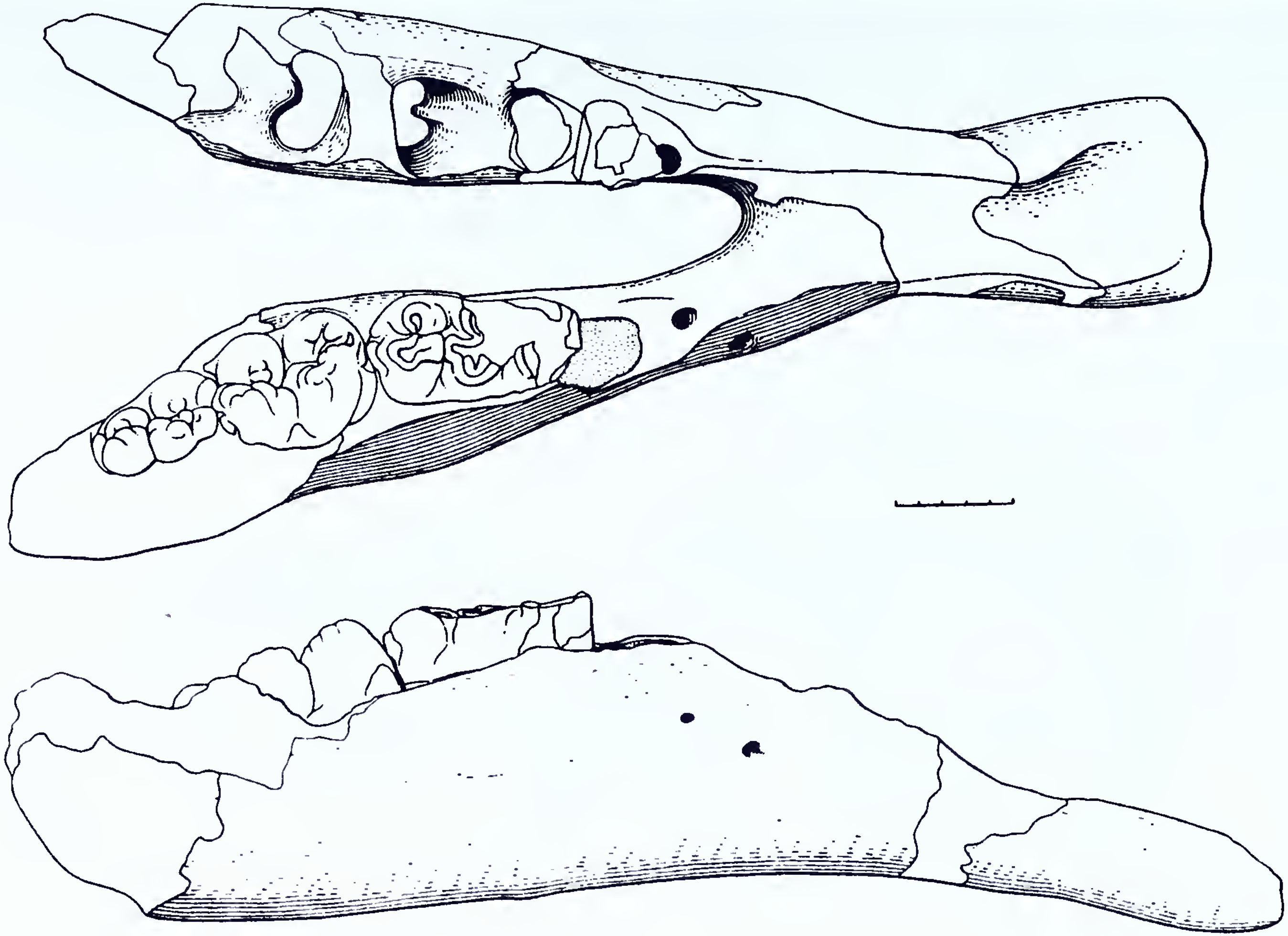

Figure 1. Megabelodon minor, n. sp. Holotype, UCMP 67101. Mandible with right M_3, parts of right M_2, left M_1. Above, occlusal view; below, right side view. Scale equals five centimeters.

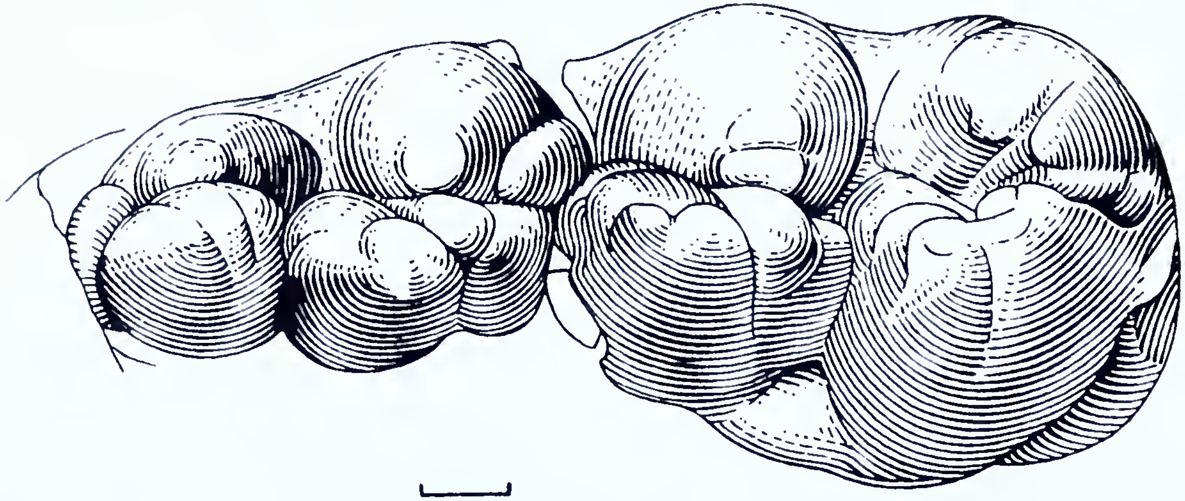

Figure 2. *Megabelodon minor*, n. sp. Holotype, UCMP 67101. Occlusal view of nearly unworn right M_3. Scale equals one centimeter.

proboscideans by the combination of characters of mandible and teeth and its small size. The character of the symphysis suggests referral to *Megabelodon*.

The presence of lower tusks is variable in some short-jawed proboscideans, such as *Mammut americanum* (Kerr). In the long-jawed mastodonts, however, the absence of lower tusks is probably more significant. The great tuskless spoon-bill of *Gnathabelodon* must surely be a part of a specialized feeding mechanism. This is equally true of the long tuskless jaws of *Megabelodon lulli* and *M. phippsi*, and, I believe, of the shorter jaw of *M. minor*. "*M.*" *cruziensis* and "*M.*" *joraki*, as already noted, may be pathologic rather than specialized. In *Eubelodon*, the long but tuskless jaw may indicate another peculiar specialization, or it may be a stage in the transition from a longirostrine to a brevirostrine condition, as implied in Osborn's placement of this genus in the ancestry of *Stegomastodon* (his *Cuvieronius*).

The dental differences among the three genera, *Megabelodon*, *Gnathabelodon*, and *Eubelodon*, indicate that they independently developed their tuskless, long-jawed condition. *Megabelodon minor* appears to be related to the Nebraska megabelodons, but it may possibly represent a fourth independent line of tuskless longirostrine gomphotheres.

The *Megabelodon minor* mandible was preserved in a marly lacustrine limestone, suggesting that the animal frequented the shores of a lake, feeding on soft near-shore vegetation, as has been proposed for other shovel-tusked and spoon-billed mastodonts.

ACKNOWLEDGEMENTS

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Table 1

Comparative measurements of Megabelodon

		M. minor (type) *UCMP 67101*	*M. lulli* (type) *(Cook, 1928)*	*M. phippsi* (type) *(Cook, 1928)*	"*M.*" *cruziensis* (type) (Frick, 1933)
RM$_2$	length	95*	--	123	--
	width, 3rd lophid	46	--	95	--
	index, width/length	48		77	
RM$_3$	length	130*	222	232	180
	width, 1st lophid	59	89	82	--
	index, width/length	40	40	35	
	height, 1st lophid	50*			
Mandible	depth below M$_2$	100			
	width at M$_2$	66			
Symphysis	length	210*	724	673	375*
	maximum width near tip	95*			

* Estimated dimension of incomplete or inaccessible structure.

of the late Dr. R. A. Stirton. An earlier version of the manuscript was read by Dr. Heinz Tobien, who offered valued suggestions and information.

The illustrations are by Owen J. Poe.

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PALEOBIOS

Contributions from the University of California
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No. 5 June 1, 1968

BRACKISH WATER OSTRACODS FROM LA JOLLA SUBMARINE CANYON 7200 ± 500 YEARS BEFORE PRESENT

by

John C. Holden

no. 5

BRACKISH WATER OSTRACODES FROM LA JOLLA SUBMARINE CANYON, 7200 ± 500 YEARS BEFORE PRESENT

BY JOHN C. HOLDEN

The occurrence of the ostracode *Perissocytheridea meyerabichi* in the Holocene offshore of Southern California sheds some light on the paleoecology of the cliff forming strata of La Jolla submarine canyon described by Shepard and Dill (1966). The material was collected by Robert F. Dill from the headward cliff of La Jolla submarine canyon at a depth of 23 meters. A date of 7200 ± 500 Y.B.P. on the strata has been determined by the carbon 14 analysis of a large root (Shepard and Dill, 1966, p. 57). After the discovery of fossils, the entire "lagoonal" section was recollected by Dill and the writer at approximately 10 foot (3.5 m.) intervals at 27.5 m., 24.5 m., 21.5 m., 18.0 m., and 16.0 m. below sea level. These horizons were mostly barren with only a few foraminifers and ostracodes at 27.5 m., 21.5 m., and 16.0 m. intervals.

Other organisms occurring with *Perissocytheridea meyerabichi* include:

Ostracoda	*Ambostracon diegoensis* (LeRoy, 1943)
	Cythere maia (Benson, 1959)
	Caudites fragilis LeRoy, 1943
	Cushmanidea sagena Benson & Kaesler, 1963
	Loxoconcha lenticulata LeRoy, 1943
	Mutilus (Aurila) lincolnensis (LeRoy, 1943)
Ectoprocta	*Bicrisia edwardsiana* (d'Orbigny)
	Thalamoporella sp.
	Scrupocellaria sp.
	Hornera sp.
Foraminifera	*Cibicides fletcheri* Galloway
	Dyocibicides biserialia Cushman & Valentine
	Nonionella basispinata (Cushman & Moyer)
	Elphidium translucens Natland
	"*Rotalia*" sp.
	Discorbis sp.
	Pseudopolymorphina sp.
	Triloculina sp.

Gastropoda	Caecum californicum Dall
Rhodophyta	Jania subpinnata Dawson

PALEOECOLOGY

Perissocytheridea is one of a few ostracode genera that appears restricted to brackish water environments (Moore, 1961; Sandberg, 1964). Species of this genus can be found in bays and estuaries with salinities approaching those of normal sea water but they do not live in abundance in the normal marine environment. The genus is unknown in Southern California waters today even though there are several bays and estuaries in this area in which it might be expected to live.

The collection of fossil Perissocytheridea consists of 27 specimens of which 25 are from the root locality and two from the minus 16.0 meter horizon containing only P. meyerabichi. At the root locality, containing the ostracode-foram-bryozoan fauna listed above, P. meyerabichi represents almost half of the ostracode fauna. This high relative abundance suggests a brackish water or polyhaline environment of deposition. The specimens appear autochthonous in view of their excellent preservation. Most have both valves intact and there are few young. If the assemblage was redeposited, one would expect a higher percentage of the more hydrodynamically susceptible smaller young and single-valve specimens than is actually encountered.

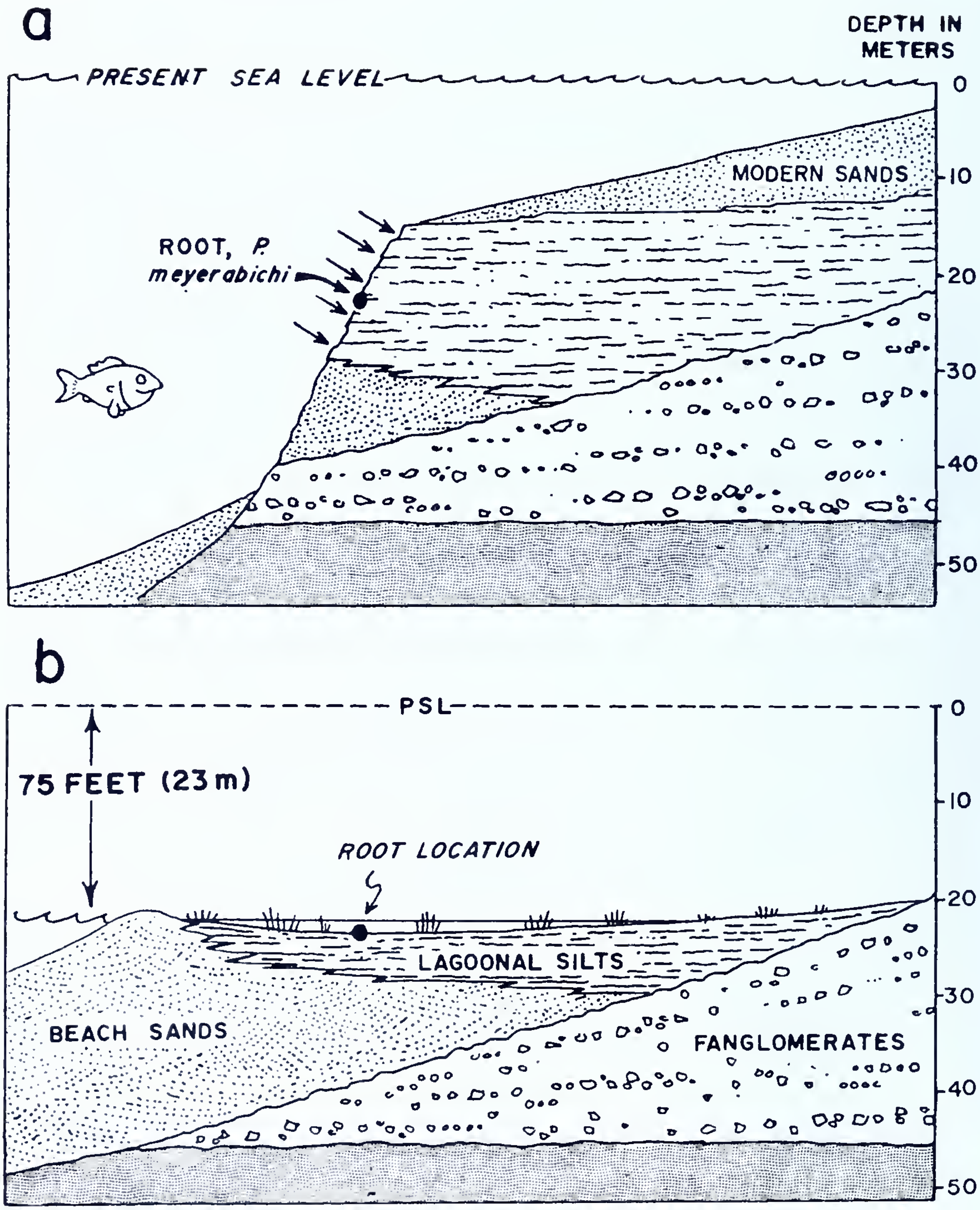
The sedimentary section consists of fine-grained silty clays with abundant reeds and a few large pieces of wood which were interpreted as lagoonal in origin by Shepard and Dill (1966). The presence of abundant well preserved Perissocytheridea meyerabichi, most with both valves intact, supports this interpretation. The paleoenvironmental aspect of the total fauna does not argue for extremely low salinities. Most of these species can be found on the near shore waters off San Diego. Thus it would appear that deposition of these "lagoonal deposits" took place in a near normal marine environment as might be expected in a bay.

Perissocytheridea meyerabichi has also been observed in abundance by the writer in samples from an outcrop of the Pleistocene Bay Point Formation exposed in Carmel Canyon, San Diego County. The ostracode fauna accompanying it there consists of *Xestoleberis aurantia*, *Loxoconcha lenticulata*, *Puriana pacifica*, *Ambostracon diegoensis*, *Limnocythere santipatricii* and flood proportions of *Cyprideis castus*--a species of another brackish water genus. On the other hand, *Perissocytheridea meyerabichi* has not been observed in the normal marine facies of the Bay Point Formation, *e.g.*, as at the type locality of the formation at Bay Point, San Diego, California.

Perissocytheridea meyerabichi is a common brackish water element of the tropical to subtropical Sonoran Realm of Benson (1959). The species is widespread along the coast of El Salvador in Estero Jiquilisco, Estero San Diego, Estero Jalteqoue, Estero Santiago, Estero Lagune and the Gulf of Fonseca in waters ranging from freshwater to 32.2 ^{o}/oo at temperatures from 25-32°C (Hartmann, 1956). Benson and Kaesler (1963) report the species in abundance in their "upper lagoon biotype" in Estero de Tastiota, Gulf of California with salinities up to 44 ^{o}/oo and temperatures up to 34°C. They find the species sufficiently restricted ecologically to be an indicator of that biotype. Elsewhere in the Gulf of California it has been reported by Swain (1967) from four stations at 8, 18, 21, and 28 fathoms respectively. Swain lists the species in two distributional categories, (1) "general distribution" and (2) "brackish water and freshwater". In the former category he notes that the species is "reworked offshore in some areas, perhaps by floating vegetation" (Swain, 1967, p. 9). In the latter category it is the most commonly occuring species from brackish, hypersaline, and freshwater lagoonal and deltaic areas south of Mazatlan and Sinaloa (Swain, 1967, p. 11). On the west side of Baja California the species occurs in the inner lagoon of Laguna Ojo de Liebre in the Bahia Sebastian Viscaino area in salinities from 37-42 ^{o}/oo and temperatures from 19-27°C (McKenzie and Swain, 1967).

Figure 1 -- Geological cross-sections through the area of La Jolla submarine canyon. a, Present day conditions near the head of the canyon. Horizons collected for microfossils using SCUBA indicated by arrows. b, Reconstruction of the environment of deposition at the time of deposition of the root dated at 7200± 500 Y.B.P. The microfauna accompanying _P. meyerabichi_ is indicative of near normal salinity inferring that the beach sands were not acting as a complete barrier between the lagoon and the sea.

no. 5


a
DEPTH IN METERS
PRESENT SEA LEVEL
0
MODERN SANDS
10
ROOT, P. meyerabichi
20
30
40
50
b
PSL
0
75 FEET (23 m)
10
ROOT LOCATION
20
LAGOONAL SILTS
30
BEACH SANDS
FANGLOMERATES
40
50

SYSTEMATIC PALEONTOLOGY

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDEIDAE Sars, 1925
Genus PERISSOCYTHERIDEA Stephenson, 1938
Perissocytheridea meyerabichi (Hartmann, 1953)
Figs. 2a-c

Iliocythere meyer-abichi Hartmann, 1953, p. 310-314, figs. 1-10; 1957, p. 141.

Perissocytheridea meyerabichi (Hartmann, 1953). Benson and Kaesler, 1963, p. 17, pl. 4, figs. 1-5, text-fig. 7; McKenzie and Swain, 1967, p. 286, pl. 29, fig. 4; Swain, 1967, p. 53, pl. 4, figs. 7a-b, 8a-c; pl. 8, figs. 1a-d; text-figs. 4-f-i, 44c-d.

Diagnosis: A species of *Perissocytheridea* with a relatively subquadrate outline viewed from the side; caudal process bluntly pointed, near posteroventer; shell elongate, coarsely but not strongly reticulate.

Description: Sexes strongly dimorphic: males longer and lower than females; male length/height=2.00, female length/height=1.80. Carapace ornamented with 8 to 9 horizontal ridges over which less conspicuous vertical ridges form a coarse reticulate pattern. Surface heavily pitted, pits pronounced in mid-regions of valves, inconspicuous at extremities. Short sulcus behind low, barely discernible, eye tubercal, lesser sulci behind it. Posterodorsal region slightly inflated with resulting arcuate trend of horizontal ridges. In dorsal view, greatest width in posterior third (male) or at mid-length (female). Radial pore canals sparce, very fine, about 10 in anterior, five in posterior. Normal pores sparce, large, sieve type. Hinge antimerodont tending to entomodont: median bar of left valve crenulate, anterior half more coarsely crenulate with 12-15 toothlets. Posterior and anterior elements of right valve each with six toothlets. Adductor muscle scar pattern of four vertically arranged scars astride a subcentral vertical swelling. Anteriorly opened "V" shaped frontal scar in front and above adductor scar group.

Discussion: Small differences in the carapace exist between the La Jolla Canyon specimens off San Diego and living representatives described by Hartmann (1953) and by Benson and Kaesler (1963). Specimens from the Gulf of California (Benson and Kaesler, 1963) have more toothlets in the anterior element (seven) and fewer in the posterior element (five). In addition, the dorsomedian sulcus is well developed whereas in the La Jolla Canyon specimens several sulci are present along the anterodorsal margin. Hartmann (1953) shows the female to be somewhat more triangular in outline and to have a higher more pointed caudal process than the La Jolla Canyon specimens. Otherwise they appear to be identical.

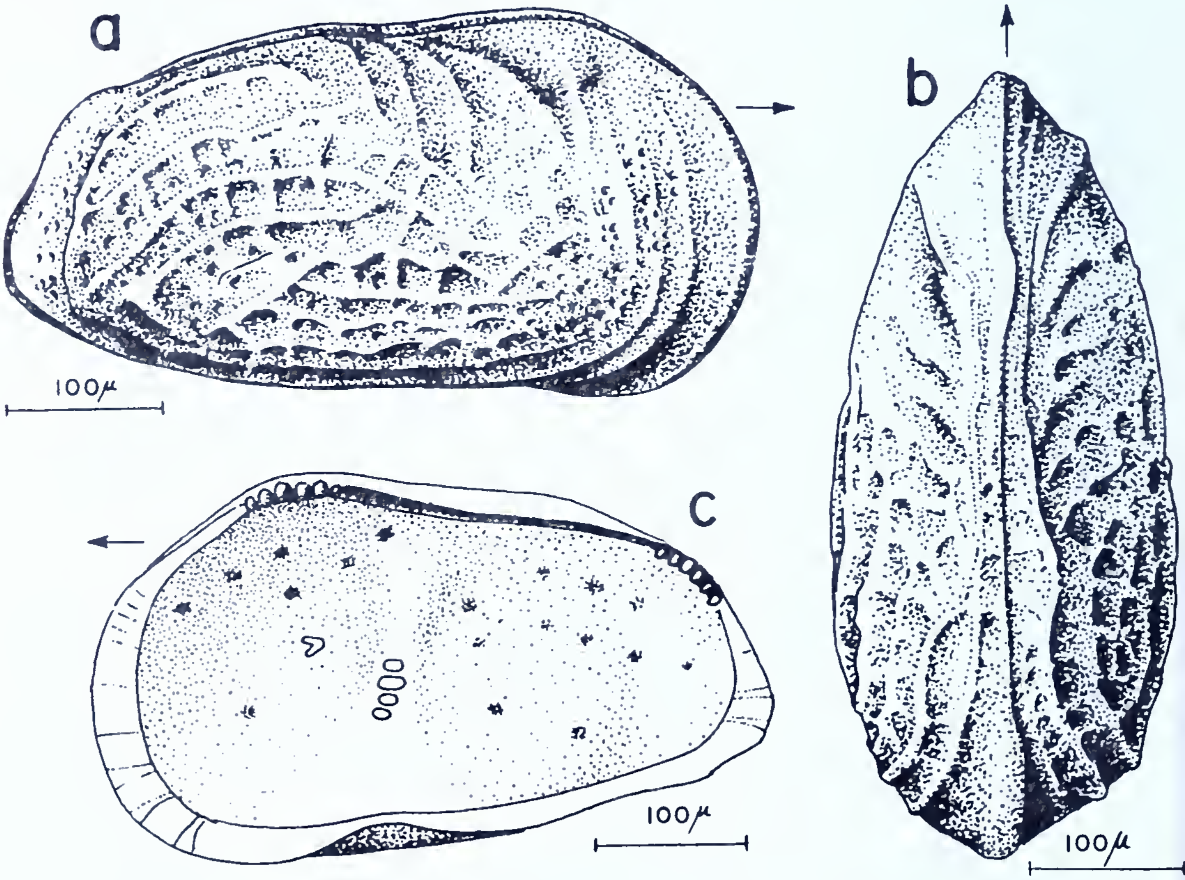


Figure 2 -- Perissocytheridea meyerabichi (Hartmann, 1953); a, external view of right valve male, hypotype United States National Museum specimen USNM 650928. b, Same specimen, dorsal view. c, Internal view of right valve female, hypotype USNM 650929.

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PALEOBIOS

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 6 October 15, 1968

RODENTS FROM THE HARTMAN RANCH LOCAL FAUNA, CALIFORNIA

by

Everett Lindsay

RODENTS FROM THE HARTMAN RANCH LOCAL FAUNA, CALIFORNIA

BY EVERETT LINDSAY

ABSTRACT

Fossil rodents, represented by approximately 140 isolated teeth, were collected from the lower part of the Sespe Formation near Sespe Gorge, Ventura County, California. Age of the fauna is Uintan. The Hartman Ranch small mammal fauna includes *Pareumys* sp., *Namatomys fantasma* n. sp., *Griphomys* sp., and *Simimys* sp.

Namatomys fantasma shares morphological features with *Simimys*, suggesting these forms are phyletically related. *N. fantasma* has cheek tooth formula (4/4) identifying it as an eomyid while *Simimys* has cheek tooth formula (3/3) identifying it as a cricetid. Teeth of *N. fantasma* also resemble those of some sciuravids and zapodids, suggesting *N. fantasma* is intermediate in a lineage Sciuravidae ⟶ Eomyidae ⟶ Cricetidae and Zapodidae.

Pareumys and *Griphomys* are presently represented by only a few specimens.

INTRODUCTION

Fossils from Hartman Ranch, UCMP locality V-5814, Ventura County, California, include cylindrodontid, eomyid, ?geomyid, and cricetid rodents. Well-diversified small mammal faunas were previously reported from the Lower Sespe Formation by Chester Stock (1935), R. W. Wilson (1935, 1940A, 1940B, 1940C, 1949), and A. E. Wood (1956). Earlier described late Eocene faunas from the Sespe Formation were from sites in the Simi foothills near Fillmore, California. This is the first report of small mammals from the Sespe Formation near Sespe Gorge.

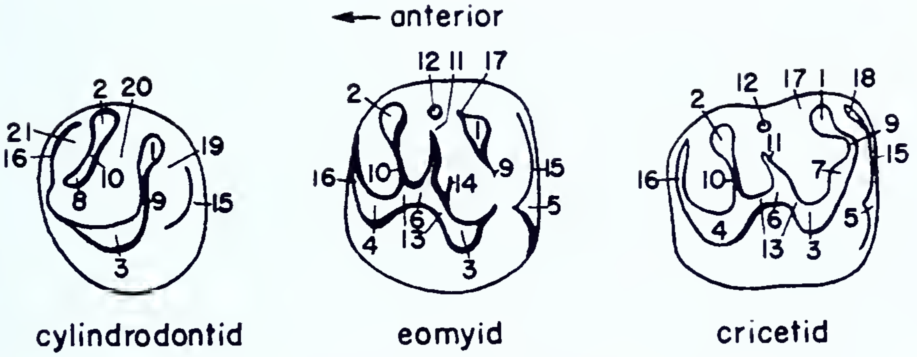

Figure 1. Cusp terminology in upper cheek teeth

1-Paracone
2-Metacone
3-Protocone
4-Hypocone
5-Anterocone
6-Mesocone
7-Protoconule

8-Metaconule
9-Protolophule
10-Metalophule
11-Mesoloph
12-Mesostyle
13-Mure
14-Posterior arm of protocone

15-Anterior cingulum
16-Posterior cingulum
17-Labial loph
18-Parastyle
19-Anterior basin
20-Central basin
21-Posterior basin

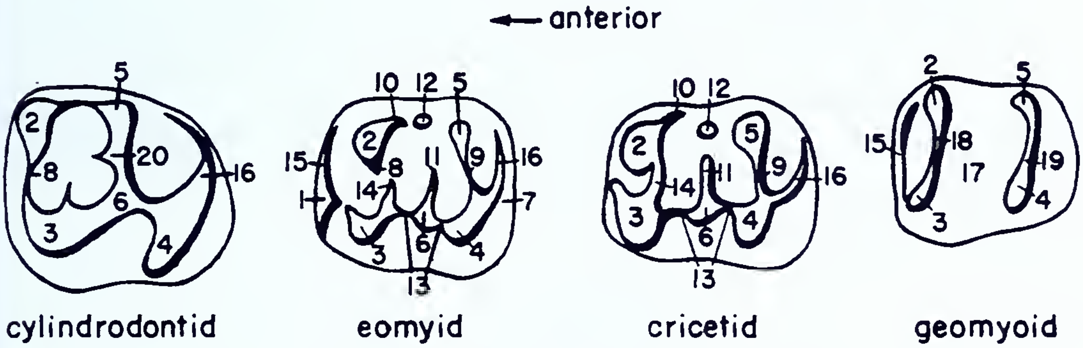

Figure 2. Cusp terminology in lower cheek teeth

1-Anteroconid
2-Metaconid
3-Protoconid
4-Hypoconid
5-Entoconid
6-Mesoconid
7-Posteroconid

8-Metalophulid
9-Entolophulid
10-Lingual lophid
11-Mesolophid
12-Mesostylid
13-Mure
14-Posterior arm of protoconid

15-Anterior cingulum
16-Posterior cingulum
17-Transverse valley
18-Metalophid
19-Hypolophid
20-Transverse lophid

Fossils were collected from calcareous, green, thin lenses of coarse-grained sandstone within the red shales near the base of the Sespe Formation. The sandstone lenses are lithologically similar to the Coldwater Sandstone that underlies the Sespe Formation and suggest local intertonguing of the Lower Sespe Formation with characteristic Coldwater Sandstone.

Tortoise and rhinocerotoid fossils were collected from the Hartman Ranch locality also.

Age of the Hartman Ranch local fauna is Uintan (late Eocene), correlative with the Tapo Ranch fauna, based on morphological similarity of *Simimys* sp. and *Pareumys* sp. from Hartman Ranch and the Tapo Ranch fauna.

The rodent specimens were collected by underwater screenwashing using two sets of screen, 18-mesh and 25-mesh. Some of the matrix was digested with dilute acetic acid prior to screening.

The following abbreviations are used in the text. UCMP = University of California Museum of Paleontology; LACM(CIT) = Los Angeles County Museum, collections formerly catalogued at the California Institute of Technology. All measurements are in millimeters.

Figures 1 and 2, above, illustrate the position of morphologic terms used in the descriptions of rodent teeth.

SYSTEMATICS

Order RODENTIA

Family CYLINDRODONTIDAE Miller and Gidley 1918

Pareumys Peterson 1919

Pareumys sp.

Three isolated, relatively high-crowned cheek teeth, ?RP^4 (UCMP 79271), ?LM^3 (UCMP 79272), and LM_3 (UCMP 79477) are identified as *Pareumys* sp. The premolar and M_3 are relatively unworn, with the posterolabial corner broken away on both teeth. M^3 is well worn.

Description of material: ?P^4 - oval occlusal outline; paracone and metacone relatively close, metacone slightly labial relative to paracone; protolophule long, directed transversely, strongly united to long and narrow protocone that is continuous with posterior cingulum; metalophule short, terminating medially, with weak union to posterior cingulum; central basin deep and wide; anterior basin deep and narrow; anterior cingulum low, continuous from protocone to termination anterior to paracone; parastyle absent.

?M^3 - subquadrate occlusal outline, with anterolabial expansion; enamel island in posterior half of tooth; island transversely elongate with anterior and posterior sides convex anteriorly.

M_3 - oval occlusal outline; metaconid and protoconid prominent; hypoconid probably prominent (broken); entoconid small, mesoconid minute; metaconid and entoconid opposite anterior arm of labial cusps; anterior arm of protoconid high, directed transversely to its union with the metaconid; median transverse lophid (?mesolophid) high, uniting mesoconid and entoconid; posterolingual cingulum high, continuous from metaconid to posterior arm of hypoconid, passing through entoconid; isolated anterior and posterior lakes, separated by median transverse lophid; anterior lake deeper and wider than posterior lake; small lophule projecting into anterior lake from median protoconid, small lophule projecting anteriorly into anterior lake from medial region of transverse lophid; anteroconid and anterior cingulum absent.

Discussion: *Pareumys* sp. from Hartman Ranch is relatively high-crowned; occlusal measurements (Table 1) are comparable to other specimens of *Pareumys* from the Sespe Formation (Wilson, 1940C). The Hartman Ranch P^4 is distinguished from *Cylindrodon* by its short metalophule.

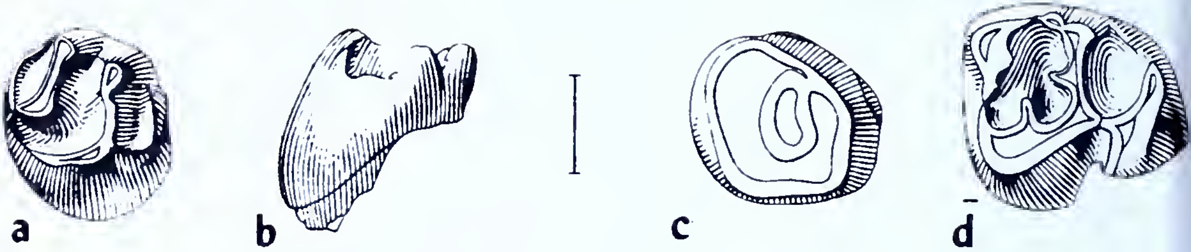

Figure 3. *Pareumys* sp. *a-b*. UCMP 79271, ?RP^4 (*a*. occlusal view, *b*. anterior view); *c*. UCMP 79272, ?LM^3 occlusal view; *d*. UCMP 79477, LM$_3$ occlusal view. (scale line = 1 mm.)

Family EOMYIDAE Depéret and Douxami 1902

Namatomys Black 1965

Two species of *Namatomys* are presently known. *N. lloydi* is known from two mandibles collected at the early Oligocene Pipestone Springs locality in Montana. One mandible has a complete dentition, the other is missing the M$_3$. *N. fantasma* n. sp. from the Hartman Ranch local fauna is known only from isolated cheek teeth. Precise dental formula is essential for taxonomic identification since eomyids have cheek tooth formula 4/4, sciuravids have 5/4, fossil zapodids have 4/3, and cricetids have 3/3. All the families named above have low-crowned, lophate cheek teeth. The most significant characters uniting *N. fantasma* with *N. lloydi* are presence of an anteroconid on P$_4$, and cheek tooth formula.

*Namatomys fantasma** n. sp.

Type: UCMP 77660 RP4, V-5814 Hartman Ranch, Ventura County, California.

Hypodigm: Type and UCMP 66986-66988, 77648-77650, 77652-77654, 77656-77670.

Stratigraphic and geographic range: Lower Sespe Formation in Sespe Gorge, Ventura County, California.

Age: Uintan (late Eocene).

Diagnosis: Anterocone (-id) on all cheek teeth except P^4; lower cheek teeth longer than wide; anterior arm of protoconid not elongated transversely to base of metaconid; metalophulid and entolophulid unite with posterior arms of protoconid and hypoconid; upper cheek teeth wider than long; paralophule and metalophule unite with anterior arm of lingual cusps; mesocone (-id) minute on all cheek teeth, except absent on M^1 and M^3; M^3 reduced posteriorly.

Differential diagnosis: *Namatomys fantasma* differs from *Namatomys lloydi* in stronger development of posterior metalophulid and weaker development of anterior arm of protoconid. *N. fantasma* differs from *Simimys* sp. from the Hartman Ranch fauna in possessing four upper and lower cheek teeth, smaller external dimensions, upper cheek teeth wider than long, and stronger development of mesocone (-id). *Namatomys* is the only known eomyid rodent with an anteroconid on P_4.

Sciuravus powayensis from the Poway conglomerate in San Diego County, California, is similar to *N. fantasma* but lacks an anteroconid on P_4 and has five upper cheek teeth. P^4 of *N. fantasma* lacks an appression facet on its anterior vertical face.

Description: dP^4 - paracone and metacone opposite the protocone and hypocone; posterior arm of protocone directed transversely, extending to median plane; protolophule and metalophule directed lingually,

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*Etymology: *fantasma* (L.) = ghost, phantom; referring to absence of associated material, hence an amorphous nature.

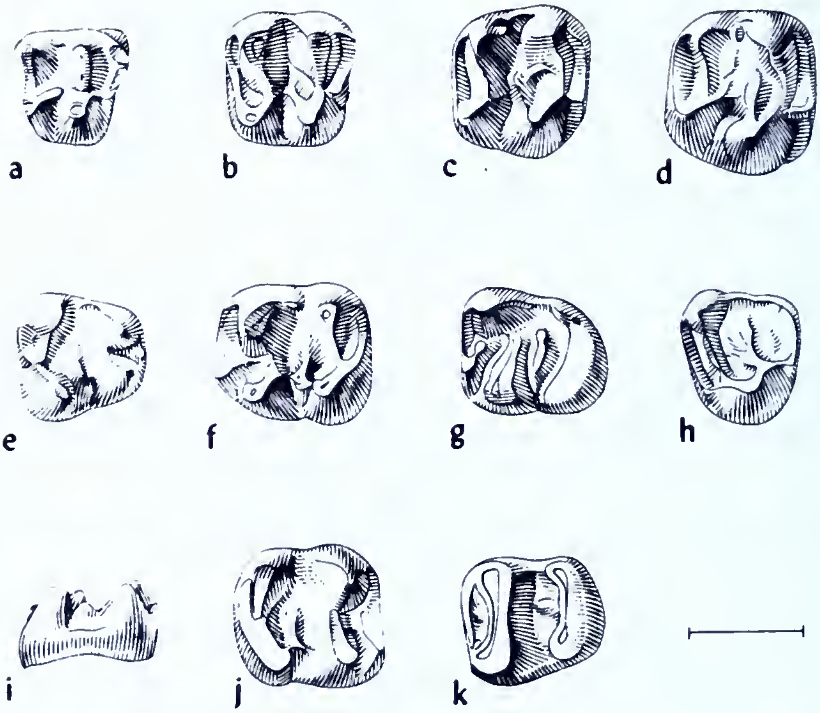


Figure 4. *a-j*. *Namatomys fantasma* new species. *a*. UCMP 79504, RdP^4 occlusal view. *b*. UCMP 77648, RP^4 occlusal view. *c*. UCMP 77654, RM^2 occlusal view. *d*. UCMP 77655, RM^1 occlusal view. *e*. UCMP 77660, RP_4 occlusal view. *f*. UCMP 77666, LM_1 occlusal view. *g*. UCMP 77668, LM_2 occlusal view. *h*. UCMP 77657, LM^3 occlusal view. *i*. UCMP 77660, RP_4 labial view. *j*. UCMP 79482, RM_2 occlusal view. *k*. *Griphomys* sp. UCMP 79479, LM_3 occlusal view. (scale line = 1 mm.)

uniting with anterior arm of lingual cusps; mesocone weakly represented by medial thickening on mure; mure between protocone and hypocone, uniting both cusps; mesoloph short; mesostyle minute, weakly uniting with labial loph that is directed posteriorly from paracone; anterior cingulum weakly joining anterior arm of protocone near median plane; parastyle small, elongated transversely; posterior cingulum low, terminating at median plane; cingular shelf labial to posterior cingulum on posterior margin; protoconule absent.

P^4 - subrectangular occlusal outline, wider than long; paracone and metacone opposite anterior arm of protocone and hypocone; posterior arm of protocone directed transversely extending labial to mure in 9 of 13 specimens, weakly uniting with paracone in 3 specimens; protolophule and metalophule directed transversely, uniting with anterior arm of lingual cusps; mesocone a slight thickening along mure in 10 of 13 specimens; mure uniting protocone and hypocone in 12 of 13 specimens; mesoloph short and stub-like in 12 specimens, prominent although never reaching mesostyle in 2 specimens; mesostyle small in 8 specimens, absent in 2 specimens; labial loph directed posteriorly from paracone in 5 specimens, absent in 5 specimens; anterior cingulum uniting with anterior arm of protocone near median plane, prominent labial to point of union, weakly developed lingual to median plane; posterior cingulum continuous from hypocone to posterolabial corner of tooth; protoconule absent; appression facet absent from anterior vertical face.

M^1 - subrectangular occlusal outline, slightly wider than long; largest tooth in upper dental series; paracone and metacone opposite anterior arm of protocone and hypocone; posterior arm of protocone with short extension labial to mure in 7 of 11 specimens; protolophule and metalophule directed transversely and slightly curved (convex anteriorly), uniting with anterior arm of lingual cusps; mesocone not discernible on mure; mure uniting protocone and hypocone in 9 of 11 specimens; mesoloph short and low; mesostyle small in 9 specimens, absent in 2 specimens; labial loph absent; anterocone small on anterior cingulum lingual to median plane; anterior cingulum uniting with anterior arm of protocone, prominent labial to anterocone, short and low lingual to anterocone, but continuous to base of protocone; parastyle small; posterior cingulum prominent on posterior margin, continuous from hypocone to posterolabial corner of tooth; protoconule absent.

M^2 - subrectangular occlusal outline, perceptibly wider than long; shorter in length than M^1; paracone and metacone opposite anterior arm of lingual cusps; posterior arm of protocone with extension labial to mure strongly developed in 1 specimen, weakly developed in 7 specimens, and extension absent in 5 specimens; protolophule and metalophule directed transversely and curved (convex anteriorly), uniting with anterior arm of lingual cusps; mesocone a slight thickening on mure in 6 of 11 specimens, absent in 5 specimens; mure uniting protocone and hypocone in 10 specimens; mesoloph short in 10 of 13 specimens; mesostyle small; labial loph directed posteriorly from paracone in 2 of 11 specimens; anterocone small, lingual to median plane where anterior cingulum unites with anterior arm of protocone in 10 of 12 specimens; anterior cingulum prominent labial to anterocone, weakly developed lingual to anterocone; parastyle minute; posterior cingulum prominent on posterior margin, continuous from hypocone to posterolabial corner of tooth.

M^3 - subrectangular occlusal outline, slightly wider than long; smallest tooth in upper dental series; paracone and protocone prominent; hypocone minute; metacone absent; protolophule directed transversely, curved (convex anteriorly), uniting with anterior arm of protocone; central basin shallow, bounded anteriorly by paracone, protolophule, and protocone, bounded posteriorly by low posterior cingulum; posterior cingulum continuous along labial margin, uniting with base of paracone; mesoloph and mesostyle absent; anterocone minute on anterior cingulum where cingulum joins anterior arm of protocone; anterior cingulum long and narrow labial to anterocone, short and low lingual to anterocone; parastyle minute.

P_4 - obovate occlusal outline, narrow anteriorly; smallest tooth of lower dental series; anteroconid minute, isolated on medial plane in 9 of 10 specimens; metaconid transversely opposite and united posteriorly to protoconid by lateral extension of posterior arm of protoconid; entoconid transversely opposite and united to hypoconid by transversely-directed entolophulid that contacts posterior arm of hypoconid; mesoconid small, on mure; mure uniting protoconid and hypoconid on labial side of tooth; mesolophid short; mesostylid small, present on 9 of 10 specimens; lingual lophid low, directed posteriorly from metaconid, weakly joining mesostylid in 8 of 9 specimens; anterior cingulum absent; posterior cingulum continuous from posterior arm of hypoconid near median plane to posterolingual corner of tooth; posteroconid isolated in 1 specimen.

M_1 and M_2 - rounded rectangular occlusal outline, longer than wide; largest tooth of lower dental series; anteroconid small, labial to median plane, weakly uniting with anterior arm of protoconid in 15 of 19 specimens, strongly uniting with metaconid in 3 specimens; metaconid and entoconid opposite protoconid and hypoconid and connected with posterior arm of labial cusps by transversely-directed metalophulid and entolophulid; mesoconid on mure, labial to median plane; mure weakly contacting protoconid and hypoconid in 16 of 19 specimens; mesolophid short; mesostylid minute, weakly contacting lingual lophid directed posteriorly from metaconid; anterior cingulum continuous from metaconid to protoconid, high lingual to anteroconid, low labial to anteroconid; posterior cingulum continuous from posterior arm of hypoconid to posterolingual corner of tooth.

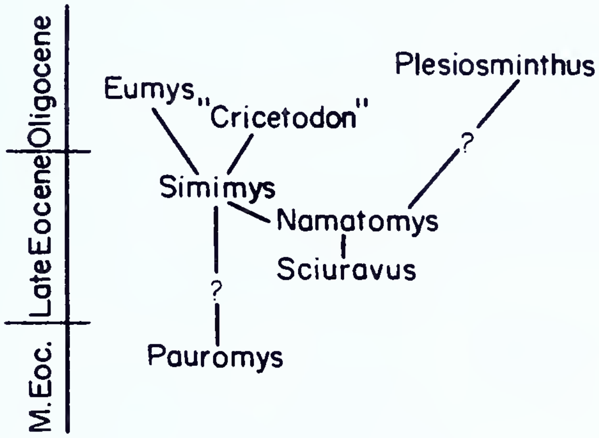
M_3 - subrectangular occlusal outline, straight anterior surface, rounded posteriorly; anteroconid small in 15 of 18 specimens; anteroconid uniting with protoconid in 7 specimens, uniting with metaconid in 3 specimens, separate from protoconid and metaconid in 5 specimens; metaconid opposite protoconid, uniting posteriorly with transversely-directed posterior arm of protoconid; entoconid opposite and strongly uniting with hypoconid by curved, wide posterior cingulum (extension of posterior arm of hypoconid); entolophulid discernible as anterior branch of posterior cingulum in 7 of 18 specimens; mesoconid small, isolated in 13 of 18 specimens, weakly contacting hypoconid in 5 specimens; mesolophid long, not reaching mesostylid on lingual margin; mesostylid minute on 11 of 17 specimens, absent on 6 specimens; lingual lophid low, directed posteriorly from metaconid in 5 of 17 specimens; anterior cingulum continuous and relatively straight between protoconid and metaconid, low labial to median plane.

Discussion: *Namatomys* is the only known eomyid with an anteroconid on P_4. Cricetid and zapodid rodents commonly have an anteroconid on the anterior lower cheek tooth identified as M_1 rather than P_4. *Simimys* sp. from the Hartman Ranch local fauna has a distinctive median anteroconid on the anterior lower cheek tooth, designated M_1. The P_4 of *Namatomys* and M_1 of *Simimys* are very similar, especially in the narrow anterior occlusal outline, small median anteroconid, absence of anterior cingulum, posterior union of protoconid and metaconid, and distinct mesoconid. It is suggested that P_4 of eomyid rodents and M_1 of cricetid rodents may be homologous elements in the dental series. A general trend observed in middle Tertiary and later cricetid rodents is increased size of the anterior lower cheek tooth and reduction of the posterior lower cheek tooth. Solution to homology of lower cheek teeth in cricetid and other rodents awaits additional collecting, especially in late Eocene deposits.

The sample of *N. fantasma* includes 12 P_4, 27 M_1 and M_2, and 20 M_3. Number of teeth represented is probably biased by the collecting method (screen-washing), and the size of the screen relative to the size of the tooth. In the lower dental series, P_4 is the smallest tooth, and M_3 is the largest tooth. The M_1 and M_2 of *N. fantasma* are indistinguishable although in *N. lloydi* the M_1 is slightly narrower anteriorly relative to M_2.

Sciuravids, cricetids, zapodids and most eomyids have the paracone and metacone of upper cheek teeth uniting with the anterior arm of the protocone and hypocone while the metalophulid and entolophulid of the lower cheek teeth unite with the posterior arm of the protoconid and hypoconid, as in *Namatomys* and *Simimys*. In *N. fantasma* the upper cheek teeth are wider than long, as in sciuravids and some zapodids; in *Simimys* and later cricetids the upper cheek teeth are longer than wide. Development of cusps and connections between the cusps on *N. fantasma* and *Simimys* sp. from Hartman Ranch suggest a close phyletic relationship. *Namatomys* seems a probable ancestor to the cricetids and zapodids, and *Simimys* is probably the earliest cricetid.

Phyletic Relationships of Namatomys and Simimys



Late Eocene radiation of Nearctic rodents might include the transition of *Sciuravus powayensis* with cheek tooth formula 5/4 and absence of anteroconid on P_4; to *Namatomys fantasma* with cheek tooth formula 4/4 and presence of an anteroconid on P_4; to *Simimys* with cheek tooth formula 3/3 and presence of an anteroconid on the anterior lower cheek tooth. These three genera mark a transition from Sciuravidae to Eomyidae to Cricetidae.

Family GEOMYIDAE (?) Gill 1872

Griphomys Wilson 1940

Griphomys sp.

Figure 4

One complete M_3 and another isolated fragmentary lower cheek tooth have two well-developed transverse lophs. These teeth resemble illustrations and descriptions of *Griphomys*, and are unlike other rodent teeth in the Hartman Ranch local fauna.

M_3 is undescribed in *Griphomys*; the Hartman Ranch specimen, UCMP 79479, is considered M_3 because it is bilophodont and brachyodont, talonid is narrower than trigonid, and the posterior surface is rounded without an appression facet. In addition, anterior cingulum is present; posterior cingulum and mesoconid are absent; vestige of a low, short lophid is present between the anterior cingulum and the protolophid about half-way between the protoconid and median plane. Another short vestige of a lophid is directed anteriorly from the metalophid along the median plane. This tooth has the same size (Table 1) as other specimens of *Griphomys* from the Sespe Formation. In addition to *Griphomys* specimens from Hartman Ranch, the genus is known only from the Tapo Ranch fauna (*Griphomys alecer* at LACM(CIT) 207 and *Griphomys* near *alecer* at LACM(CIT) 202) and the Pearson Ranch fauna (*Griphomys* near *alecer* at LACM(CIT) 150) in the Sespe Formation.

Family CRICETIDAE Rochebrune 1883

Simimys Wilson 1935

Wilson (1949) noted the following characters of *Simimys*: (a) presence of well-developed anterior cingula and anterior protocone crests in upper cheek teeth; (b) a small thickening on the anterior cingula of upper cheek teeth; and (c) cheek tooth formula 3/3. *Simimys* is known only from the Sespe Formation: *S. murinus* from LACM(CIT) locality 180, *S. vetus* from LACM(CIT) locality 207, *S.* cf. *vetus* from LACM(CIT) locality 202, *S. simplex* from LACM(CIT) locality 150, Simimys sp. from LACM(CIT) locality 127, and Hartman Ranch UCMP locality V-5814.

Simimys sp.

Simimys sp. from Hartman Ranch is represented by nine isolated cheek teeth. They are one M_1, two M_2, three M_3, and three upper cheek teeth, probably M^2. Upper dentition of Simimys is based primarily on a skull (LACM 3529) with M^1 in place and alveoli for only M^{2-3}. Upper cheek teeth from Hartman Ranch have appression facets on the anterior vertical faces, excluding them from identification as M^1.

Description of material: M^2 - subrectangular occlusal outline, longer than wide, slightly narrower posteriorly; anterocone minute, lingual to median plane on anterior cingulum; occlusal facet on anterior and posterior vertical faces; paracone opposite anterior arm of protocone, uniting anteriorly with transversely-directed anterior arm of protocone by low, weak protolophule; protoconule minute, a local thickening on anterior arm of protocone near median plane; posterior arm of protocone directed transversely, uniting with mure at base of mesoloph; metacone opposite hypocone and uniting with anterior arm of hypocone by low, transversely-directed metalophule; anterior arm of hypocone directed anterolabially as mure; posterior arm of hypocone directed transversely as low, wide posterior cingulum; posterior cingulum continues to base of metacone; mesocone a slight thickening at base of mesoloph on 1 specimen, absent on other specimen; anterior cingulum narrow, high labially and low lingually, continuous from paracone to protocone; parastyle minute, at termination of anterior cingulum, uniting with anterior arm of protocone in 1 of 3 specimens.

M_1 - obovate occlusal outline, narrow anteriorly; anteroconid small, isolated on median plane, symmetrically located anterior to and between metaconid and protoconid; metaconid opposite and equal in size to protoconid, united posteriorly with transversely-directed

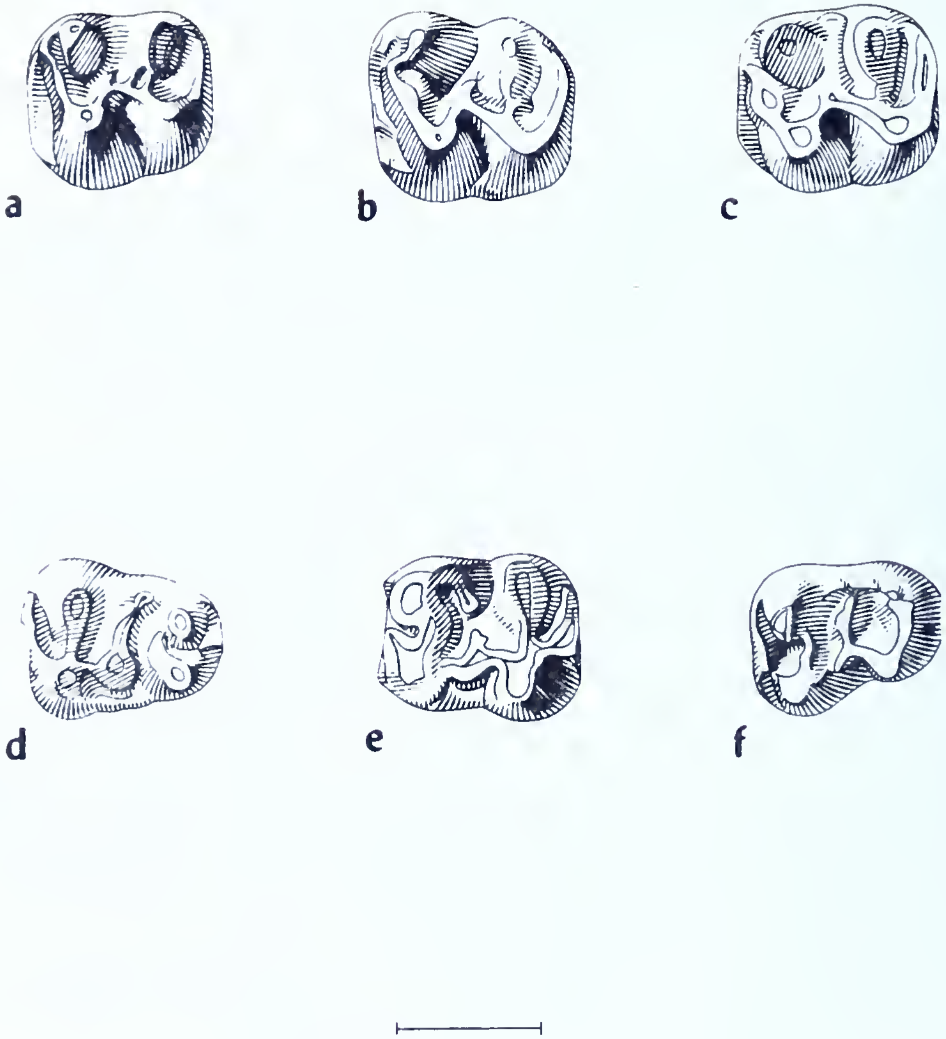


Figure 5. *Simimys* sp. *a*. UCMP 79270, LM^2. *b*. UCMP 79646, LM^2. *c*. UCMP 79269, LM^2. *d*. UCMP 79267, RM$_1$. *e*. UCMP 79268, LM$_2$. *f*. UCMP 77647, LM$_3$. (scale line = 1 mm.) All occlusal views.

posterior arm of protoconid; entoconid opposite hypoconid and united to medial hypoconid by transversely-directed and slightly curved (convex anteriorly) entolophulid; mesoconid small, united to hypoconid by posterior mure, not contacting protoconid; mesolophid long, directed transversely and flexed anteriorly, united to prominent mesostylid; mesostylid on lingual border, posterior and adjacent to metaconid; lingual lophid from metaconid absent; anterior cingulum absent; posterior cingulum high labially as posterior arm of hypoconid, low lingually where it terminates posterior to entoconid; ectolophid low on labial margin.

M_2 - subrectangular occlusal outline, narrow anteriorly; shorter in length and wider than M_1; anteroconid absent; metaconid opposite to and united with protoconid by transversely-directed posterior arm of protoconid; anterior arm of protoconid joining anterior cingulum; entoconid opposite hypoconid, weakly united to base of posterior arm of hypoconid by transversely-directed entolophulid; mesoconid small, strongly united to hypoconid, weakly united to protoconid; mesolophid short, directed transversely and flexed anteriorly, not uniting with mesostylid; mesostylid prominent, posterior and adjacent to metaconid; lingual lophid from metaconid uniting with mesostylid; anterior cingulum narrow, continuous from metaconid to protoconid on labial border, high medially at union with anterior arm of protoconid, low laterally; posterior cingulum high medially, low lingually at termination posterior to entoconid; ectolophid absent.

M_3 - obovate occlusal outline, narrow posteriorly; slightly smaller than M_2; metaconid and protoconid prominent, hypoconid reduced; anteroconid and entoconid minute to absent; metaconid opposite protoconid and united posteriorly to transversely-directed posterior arm of protoconid; anterior arm of protoconid joining anterior cingulum medially; mesoconid absent; anterior arm of hypoconid directed obliquely to mure, uniting with mesolophid; mesolophid long, not reaching lingual lophid; mesostylid absent; posterior arm of hypoconid directed transversely and continuing around posterior margin as posterolingual lophid; lingual lophid with slight notch in occlusal surface where mesostylid would be present; anterior cingulum continuous from metaconid to protoconid on labial border; anterior cingulum high near union with anterior arm of protoconid, low laterally; ectolophid absent.

Discussion: Upper cheek teeth of *Simimys* sp. from Hartman Ranch are similar to M^1 of *S. murinus* Wilson in (a) projection of the anterior arm of the protoconid to the anterolabial corner of the tooth where it unites with the parastyle, (b) a weak protoconule directed lingually from the paracone joins the anterior arm of the protocone, and (c) a minute protoconule is present on the anterior arm of the protocone. M^2 is not known in *S. murinus*. *Simimys* sp. is similar to *S. simplex* Wilson in a paracone uniting with the anterior arm of the protocone, but a parastyle is not indicated on M^2 of *S. simplex*. *S. vetus* Wilson differs from *Simimys* sp. in development of a prominent mure crest and mesocone.

Lower cheek teeth of *Simimys* sp. are about equal in size (Table 1) to *S. simplex* and *S. vetus*. The latter two species are known from complete lower dentitions. Lower molars of *S. simplex* differ from *Simimys* sp. in absence of the isolated anteroconid on M_1, M_1 is wider anteriorly, and M_3 is wider posteriorly. Lower molars of *S. vetus* differ from *Simimys* sp. in lacking the posterior union of protoconid and metaconid, and M_3 is not reduced posteriorly. Lower teeth of *S. murinus* are not known.

Simimys sp. from Hartman Ranch appears closest to *S. murinus* but specific identification is withheld, pending collection of more material.

Simimys is probably the ancestral cricetid, based on its reduced dental formula (3/3). *Simimys* was referred to ?Cricetidae by Wilson (1935) but frequently classified as a zapodid by other authors. There is no indication in *Simimys* for a fourth upper cheek tooth, a characteristic of Tertiary zapodids. *Simimys* is similar to later cricetid rodents in the development of an anteroconid on M_1 and the reduced posterior half of M_3. The protoconule of *Simimys* is possibly homologous with the anterocone of later cricetid rodents. In theory, the anterior cingulum of M^1 would not persist after P^4 was lost, and the protoconule would expand anteriorly to occlude anterior to the anteroconid of M_1. The protoconule is prominent on M^1 of *S. murinus* and minute on M^2 of *Simimys* sp. from Hartman Ranch. All known middle and late Tertiary cricetid rodents lack a protoconule and have the anterocone uniting with the anterior arm of the protocone, similar to the union of the protoconule and the protocone in *Simimys* sp. from Hartman Ranch and *S. murinus*.

The center of radiation for cricetid rodents is uncertain. Cricetids occur in the early Oligocene of Palearctica but are absent during the same interval in Nearctica. Absence of cricetids during the early Oligocene of Nearctica is anomalous,ssince other small rodents (e.g. *Adjidaumo*, *Ischyromys*, *Heliscomys*, and *Cylindrodon*) are well represented at that time. Ecological limits of Oligocene small rodents are poorly known--*Ischyromys* was considered fossorial by Wood (1937), but recent study of uncrushed *Ischyromys* skulls by Black (1968) reveal the absence of many specializations interpreted by Wood. Evidence for ecologic replacement is lacking, although *Ischyromys* was abundant in lower and middle Oligocene deposits, terminating in late Oligocene when the cricetid *Eumys* assumed dominance.

Namatomys fantasma is a good morphological intermediate between *Sciuravus powayensis* and *Simimys* sp. Another possible ancestor of *Simimys* is *Pauromys*, a middle Eocene Nearctic sciuravid. *Pauromys* has a shortened and anteriorly narrowed P_4 that is too reduced to be ancestral to *Namatomys*. *Simimys* may be derived from *Pauromys* through the loss of P_4, but morphological similarity of anterior lower cheek teeth in *Namatomys* and *Simimys* plus the posterior reduction of the posterior lower cheek tooth in *Simimys* suggest that *Simimys* was derived from Namatomys through the loss of M_3. Presence of Simimys and its presumed ancestor, Namatomys, in the same deposit at Hartman Ranch strongly suggest the early radiation of cricetids occurred in North America.

ACKNOWLEDGEMENTS

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TABLE 1. MEASUREMENTS*

		length	width Pr.	width Hy.
Pareumys sp.				
UCMP 79271	?RP^4	1.70	1.85	
UCMP 79272	?LM^3	1.85	1.75	
UCMP 79477	LM^3	2.23	2.13	
Griphomys sp.				
UCMP 79479	LM$_3$	1.23	1.03	0.90
Simimys sp.				
UCMP 77646	LM^2	1.40	1.24	1.21
UCMP 79269	LM^2	1.39	1.25	1.19
UCMP 79270	LM^2	1.26	1.20	1.07
UCMP 79267	LM$_1$	1.45	0.75	1.06
UCMP 79268	LM$_2$	1.30	1.00	1.15
UCMP 77647	LM$_3$	1.31	1.10	0.90
UCMP 82686	RM$_3$	1.26	1.13	0.83
UCMP 82687	RM$_3$	1.15	0.88	0.72

* all measurements in millimeters

Pr. = protoloph

Hy. = hypoloph

TABLE 2. MEASUREMENTS OF *Namatomys fantasma* n. sp.*

		N	X	S	V	OR
P^4	length	11	1.19±.02	.0654	5.50	1.10-1.30
	width	12	1.26±.02	.0744	5.90	1.15-1.38
M^1	length	7	1.27±.02	.0624	4.91	1.18-1.35
	width	7	1.34±.02	.0636	4.75	1.25-1.40
M^2	length	11	1.18±.01	.0342	2.90	1.13-1.23
	width	11	1.35±.02	.0666	4.93	1.25-1.45
M^3	length	7	1.00±.04	.0956	9.56	0.90-1.20
	width	7	1.10±.04	.0944	8.58	1.00-1.25
P_4	length	9	1.16±.03	.0745	6.42	1.05-1.30
	width Pr.	9	0.79±.01	.0292	3.70	0.75-0.85
	width Hy.	9	1.06±.02	.0638	6.02	0.97-1.15
M_1	length	17	1.29±.01	.0591	4.58	1.15-1.37
and	width Pr.	15	1.19±.02	.0795	6.68	1.00-1.30
M_2	width Hy.	18	1.08±.02	.0861	7.97	0.90-1.23
M_3	length	18	1.25±.01	.0595	4.76	1.15-1.35
	width Pr.	17	1.10±.01	.0540	4.91	1.00-1.22
	width Hy.	17	0.98±.01	.0505	5.15	0.90-1.08

* all measurements in millimeters
N = number of specimens measured
X = mean of sample
S = standard deviation of sample
V = coefficient of variability
OR = observed range
Pr. = protoloph
Hy. = hypoloph

PALEOBIOS

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 7 December 30, 1968

MEGAHIPPUS AND HYPOHIPPUS
(PERISSODACTYLA, MAMMALIA)
FROM THE ESMERALDA FORMATION OF NEVADA

by

J. E. Mawby

no. 7

MEGAHIPPUS AND HYPOHIPPUS (PERISSODACTYLA, MAMMALIA) FROM THE ESMERALDA FORMATION OF NEVADA

BY J. E. MAWBY

ABSTRACT

A specimen from the Esmeralda Formation (Mio-Pliocene) of Nevada provides new information concerning the poorly known anchitheriine horse, *Megahippus* McGrew. *Hypohippus nevadensis* Merriam, from the same formation, approaches *Megahippus* in size, but lacks the characteristic megahippine specialization of the dentition

INTRODUCTION

The anchitheriine genus *Megahippus* is perhaps the least well known of the later Tertiary horses. Of the genotypic species, *M. matthewi*, only a mandible (McGrew, 1938, pp. 315-317), a maxillary fragment, and some questionably referred foot elements (Barbour, 1914) have been adequately described or illustrated. One additional species, *M. mckennai*, has been described (Tedford and Alf, 1962), based on a crushed skull of an old individual, with heavily worn dentition. Additional specimens of both species are known, but descriptions have not been published.

Specimens collected by the writer provide information on structures not previously recorded adequately, especially the highly specialized upper incisors.

Specimen and locality numbers are those of the University of California Museum of Paleontology, Berkeley.

Order PERISSODACTYLA
Family Equidae
Subfamily Anchitheriinae
Megahippus, cf. *M. matthewi* (Barbour) 1914

Material: UCMP 59271, parts of cranium and mandibles of a young adult animal: right maxillary with P^{1-3}, part of P^4, fragments of other upper cheek teeth; isolated right I^2 and I^3, probably unerupted; fragments of posterior part of cranium, poorly preserved; parts of both rami of mandible, with P_2-M_3 in place, M_3 partly erupted; isolated left I_1 and right I_2, I_2 unerupted.

Locality: UCMP loc. V-6136, Confusion Quarry. Esmeralda Formation, Mineral County, Nevada. A mile north of north end of Cedar Mountain range, 4 miles northwest of Warrior Mine. Latitude 38° 38' 24" N.; longitude 117° 53' 00" W.

Age: Clarendonian (late Miocene or early Pliocene).

Description: Lower teeth (Fig. 1): Lower incisors are large and heavy, with high lingual cingula enclosing a broad spoon-shaped basin. Strong labial cingula extend up the labial corners of the teeth nearly to the tips. The lower incisors are very similar to those in the mandible (UCMP 28841) of *M. matthewi* from the Burge fauna of Nebraska, described by McGrew (1938, pp. 315-317, fig. 5). These teeth formed the basis for much of McGrew's diagnosis of the genus *Megahippus*. Incisors of the Nevada specimen are slightly larger than those of *M. matthewi* from Burge and have more strongly developed cingula.

Lower cheek teeth are also similar to those of the Burge specimen but are slightly larger (Table 1) and higher crowned. P_4 has a well developed lingual cingulum, interrupted lingual to the entoconid. There are suggestions of a lingual cingulum at the bases of the cusps of P_3 and P_4, but not on the molars. However, strong cingular structures are developed across the lower parts of the lingual openings of the metaflexids and the entoflexids of P_3 through M_3. Heavy labial cingula are present on all the lower cheek teeth. In the molars, the metastylid and metaconid are separated at their tips by a faint groove extending 2-3 mm. down the lingual side of the tooth. A similar condition appears in the unerupted premolars of an unpublished specimen of M. matthewi from Nebraska (UCMP 29559). The metastylid is about 1 mm. lower than the metaconid in the unworn M_3, and the same difference appears to have been present in the other molars. The premolars differ from the molars in a pronounced posterior extension of the metastylid, especially in early stages of wear. P_4 is the largest of the lower cheek teeth in all dimensions. There is a regular and gradual decrease in size of the other cheek teeth, both anterior and posterior to P_4.

Upper teeth (Fig. 2): Barbour (1914a, p. 171) mentions "strong incisors" with the holotype of M. matthewi, but unfortunately these teeth have never been described or figured. Upper incisors in the holotype of M. mckennai Tedford and Alf (1962) are present but heavily worn. The two upper incisors preserved in the Cedar Mountain specimen show that these teeth in Megahippus are as unique as the lowers (Fig. 2a). Unfortunately, I^1 was not found, but I^2 and I^3 are large and scoop-shaped. I^2 bears a deep basin, which is bounded labially by the high, sharp edge of the tooth. Lingually and posteriorly, the basin is bounded by a pair of high crests, which meet in a broad V. There is a short, heavy lingual cingulum at the base of the lingual crest; the posterior crest arises at the edge of the tooth. There is a labial cingulum, most pronounced at the anterior edge of the tooth. I^3 is essentially a smaller duplicate of I^2, except that the posterior crest is weaker, and bears a fold or cuspule on its basinward face. The lingual crest is faintly serrated. Incisors of M. mckennai appear to have been similar, but much smaller, and with very weak labial cingula.

P^1 (Fig. 2b) is similar in form to the corresponding tooth of Hypohippus. It differs mainly in the presence of a strong lingual cingulum and a weaker anterolabial cingulum.

P^2 and P^3 closely resemble corresponding teeth in the type of *M. matthewi*. The state of wear is nearly equivalent in the two specimens. Lingual cingula are stronger in the Nevada specimen, and the shelf anterior to the protocone is broader, especially on P^3. P^3 has a small crochet near the flexure of the metaloph, as do P^3 and P^4 in the type of *M. matthewi*. P^2 also has a crochet, but it is weaker and more laterally placed than in P^3. There is a second spur of enamel jutting anteromedially from the metaloph near its junction with the hypocone. As in the type of *M. matthewi* each tooth has a large cuspule on the cingulum anteromedial to the hypocone.

P^4 is represented by a fragment including the anterior half of the protocone and most of the protoloph. An isolated ectoloph and part of a hypocone probably also belong to this tooth. None of these fragments shows any significant difference from P^3.

A medial half of one of the molars probably is part of M^1. This fragment has a lingual cingulum nearly as strong as those of the premolars, and a cingular cuspule larger than that on P^2 or on P^3. In the type of *M. matthewi*, the lingual cingulum of M^1 does not extend across the protocone or the hypocone. Other fragments suggest that all upper molars of the Nevada *Megahippus* had well developed lingual cingula. One fragment, apparently of the left M^3, shows a very large cingular cuspule that is more than half the size of the hypocone.

Skull: Structures that can be identified are similar to those of *Hypohippus*, but are much larger.

Discussion: The type of the genus *Megahippus* McGrew (1938) was *Hypohippus matthewi* Barbour (1914). The type material of Barbour's species, from Devil's Gulch, Brown County, Nebraska, included "the right maxilla with four perfect teeth, and the left, with three, together with strong incisors. In addition, scattered lower teeth, numerous limb bones, and several nearly complete feet were found and referred to this species." (Barbour, 1914, p. 171). Only the right maxillary fragment with P^2-M^1 and a forefoot, later referred by Osborn

(1918, p. 210) to "a species of Merychippus," were described and illustrated. McGrew's generic diagnosis was based primarily on the referred mandible from the Burge fauna. Its most distinctive features were the short, upturned symphysis and greatly enlarged, procumbent incisors.

Megahippus mckennai Tedford and Alf (1962) from Barstow provides a link in time, in size, and in structure, between M. matthewi and its unknown ancestor in or near the lineage of Hypohippus. Megahippus mckennai, M. matthewi from Nebraska, and the Nevada Megahippus form a structural series, although not a perfectly graded one. The Nevada form is about 5% larger than M. matthewi, which in turn is about 25% larger than M. mckennai (Table 1). In M. mckennai, the lingual cingulum is strong on P^2, slightly weaker on P^3, and discontinuous on P^4. In M. matthewi the cingulum is continuous and strong on P^{2-4}, but discontinuous across the protocone and hypocone of M^1. In the Nevada Megahippus the cingulum is as strong on at least one (and probably on all) of the upper molars as on the premolars. M. mckennai lacks the cingular cuspule anterolingual to the hypocone, which is present in the Nevada specimen and on P^{2-4} of M. matthewi.

Crochets appear on various upper cheek teeth of all specimens of Megahippus, as they do in advanced species of Hypohippus. This was evidently a variable character, with no taxonomic significance in the Hypohippus-Megahippus branch of the anchitheriine horses.

Differences between the Nevada Megahippus and described specimens of M. matthewi from the Great Plains may merit specific separation. However, it seems advisable to refrain from naming another species until more information is available concerning the range of variation of M. matthewi.

The specimen from Cedar Mountain is the first record of Megahippus from the Great Basin. Megahippus mckennai is recorded only from the Barstow Formation in the Mojave Desert of California. James (1963) lists but has not yet described specimens of Megahippus in Clarendonian faunas of the Cuyama Valley Badlands of California. Megahippus matthewi has been reported only in the Devil's Gulch (Barbour, 1914) and Burge assemblages (McGrew, 1938), and possibly at Big Spring Canyon, South Dakota (Gregory, 1942).

AFFINITIES OF HYPOHIPPUS NEVADENSIS

Presence of Megahippus in the Clarendonian assemblage from the Cedar Mountain area raises a question about the relationships of Hypohippus nevadensis Merriam (1913, pp. 420-427). This species was based on a specimen from UCMP loc. 1980, on the east side of Cedar Mountain, a few miles southeast of locality V-6136, and in beds of approximately the same age as those at V-6137. The type specimen (UCMP 21056) includes several parts of the skeleton, including the partly articulated limbs, but the part of most importance in characterizing the species is a maxillary fragment with dP^{2-4}. These teeth are larger but similar to the milk teeth of Hypohippus affinis, and the metaloph does not connect with the ectoloph. Merriam considered the disconnection of the metaloph to be of sufficient value for establishment of a new subgenus, Drymohippus.

Only a few additional specimens referable to Hypohippus have been collected in the Cedar Mountain area. These include a tooth fragment, an astragalus, and a questionably referred metacarpal. They may represent H. nevadensis but are not directly comparable with the juvenile type specimen.

If the type specimen of Hypohippus nevadensis and the Megahippus from Cedar Mountain (UCMP 59271) were juvenile and adult individuals respectively of the same species, and if UCMP 59271 were conclusively referable to Megahippus matthewi (Barbour), the specific name M. matthewi might be a synonym of H. nevadensis, and the generic name Megahippus McGrew (1938) would be synonymous with Drymohippus Merriam (1913). The two Nevada specimens do not appear, however, to be of the same species.

Stock (1926) described two anchitheriine horse specimens from the Esmeralda Formation in Fish Lake Valley (UCMP loc. 2804), fifty miles south of Cedar Mountain. One was a skull fragment with dP^2-M^1. Stock recognized differences in the deciduous teeth but referred this specimen to *Hypohippus nevadensis* because of the similarity in size and because the M^1 showed "characteristics which at least might be expected in M^1 of the type of *Hypohippus* (*Drymohippus*) *nevadensis*." (1926, p. 64). The other specimen was a right mandible, which he also referred to *H. nevadensis*, apparently on the basis of its large size.

The deciduous premolars of the right side of the Fish Lake Valley skull fragment (UCMP 27116) and portions of the maxillary bone were removed to reveal the permanent P^{2-4}, in order to determine relationships of *Hypohippus nevadensis* with *Megahippus*. These teeth, like the M^1, are large, only slightly smaller than those of *Megahippus matthewi*. However, they lack the characteristic lingual cingulum of *Megahippus* premolars. A weak cingulum on the lingual base of the protocone of P^2 is only slightly more pronounced than the similar faint cingulum on some premolars of a skull of *Hypohippus affinis* (UCMP 28840).

Although the mandible (UCMP 27117) also rivals *M. matthewi* in size, or at least in length of the cheek tooth series, the relatively shallow ramus and relatively long diastema indicate that it is a large *Hypohippus*, rather than a *Megahippus*. The presence of an alveolus for P_1 also supports this identification, if McGrew is correct in believing that absence of this tooth is characteristic of the genus *Megahippus*. Unfortunately the Cedar Mountain specimen of *Megahippus* casts no light on this point.

The anchitheriine horse in the Fish Lake Valley fauna is a large species of *Hypohippus*, but a question may remain about its assignment to *H. nevadensis*. As Stock recognized, there are significant differences between the deciduous dentition from Fish Lake Valley and that from Cedar Mountain. Chief among these is the good connection between the metaloph and ectoloph in deciduous premolars of the Fish Lake Valley specimen. This specimen also lacks the strong lingual cingulum on dP^2, which is present in the Cedar Mountain specimen. The milk teeth of the Fish Lake Valley horse are longer anteroposteriorly than those of the type specimen of H. nevadensis, and appear somewhat narrower, which may be the result of crushing.

There is no sure evidence relating H. nevadensis to Megahippus. Although large for Hypohippus, the H. nevadensis milk dentition is smaller than would be expected for the Nevada Megahippus. The cingulum on dP^2 may suggest affinity with Megahippus, but this is not convincing. Until more evidence is found at least two species of large anchitheriine horses in the Clarendonian of west-central Nevada are recognized: Megahippus cf. matthewi, of UCMP loc. V-6136 and Hypohippus nevadensis, Merriam's type specimen, from UCMP loc. 1980. The Fish Lake Valley Hypohippus may represent a third species or may be referable to Hypohippus nevadensis.

ACKNOWLEDGEMENTS

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Figure 1 was drawn by Owen J. Poe; figure 2 by Mrs. Augusta Lucas.

TABLE 1
COMPARATIVE MEASUREMENTS OF UPPER TEETH OF *MEGAHIPPUS*.

	Megahippus cf. *matthewi* UCMP 59271	*M. matthewi* cast of type	*M. mckennai* Tedford & Alf, 1962
I^2, length	19.5 mm.		12.6 mm.
width	20.3		a 13.5
I^3, length	12.5		
width	16.7		
P^1, length	21		17.8
width	19		12.1
P^2, length (1)	38	35	
length (2)	33	31.5	23.1
width (3)	39	35.7	29.7
P^3, length (1)	a 38	36.8	
length (2)	37	33.5	26.4
width (3)	a 45	39.9	35.3
P^4, length (1)	a 38	38	
length (2)		34	27.4
width (3)		38.5	38.2

---

a - approximate dimension
(1) length along ectoloph
(2) length across protoconule-hypostyle
(3) width at base of crown

TABLE 2

COMPARATIVE MEASUREMENTS OF LOWER TEETH OF *MEGAHIPPUS*.

	M. cf. matthewi UCMP 59271		*M. matthewi* UCMP 28841
	right	left	
I_1, length		20.4 mm.	18.7 mm.
width		28	24.5
I_2, length	17.6		16.3
width	24		21.1
P_2, length	31.5		29.1
width	20		20.7
P_3, length	35	34.5	31.7
width	24.5	24	24.7
P_4, length	36	a 35	32.5
width	26	a 26	25.0
M_1, length	34.5	a 35	31.3
width	24	23.5	24.8
M_2, length	34	a 33	29.6
width	22.5	22.5	23.5
M_3, length	a 33	a 33	31
width		a 19	19.0
P_2- P_4, length	101		92

---

a - approximate dimension

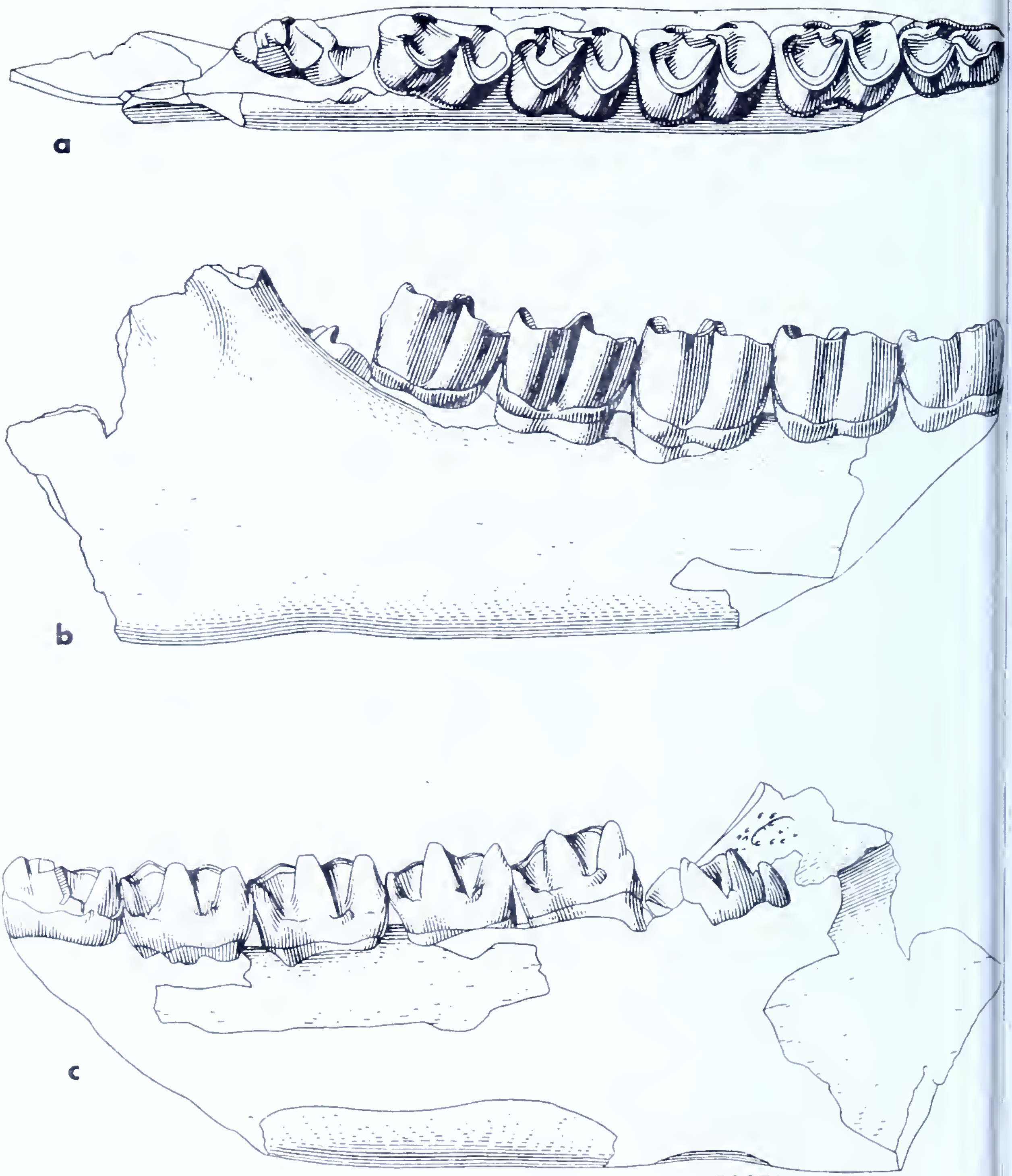

Figure 1. *Megahippus* cf. *M. matthewi*. UCMP 59271. Right ramus of mandible with P^2 - M^2 in place, M^3 erupting. *a*. Occlusal view. *b*. Lateral view. *c*. Lingual view. X 1/2.

no. 7

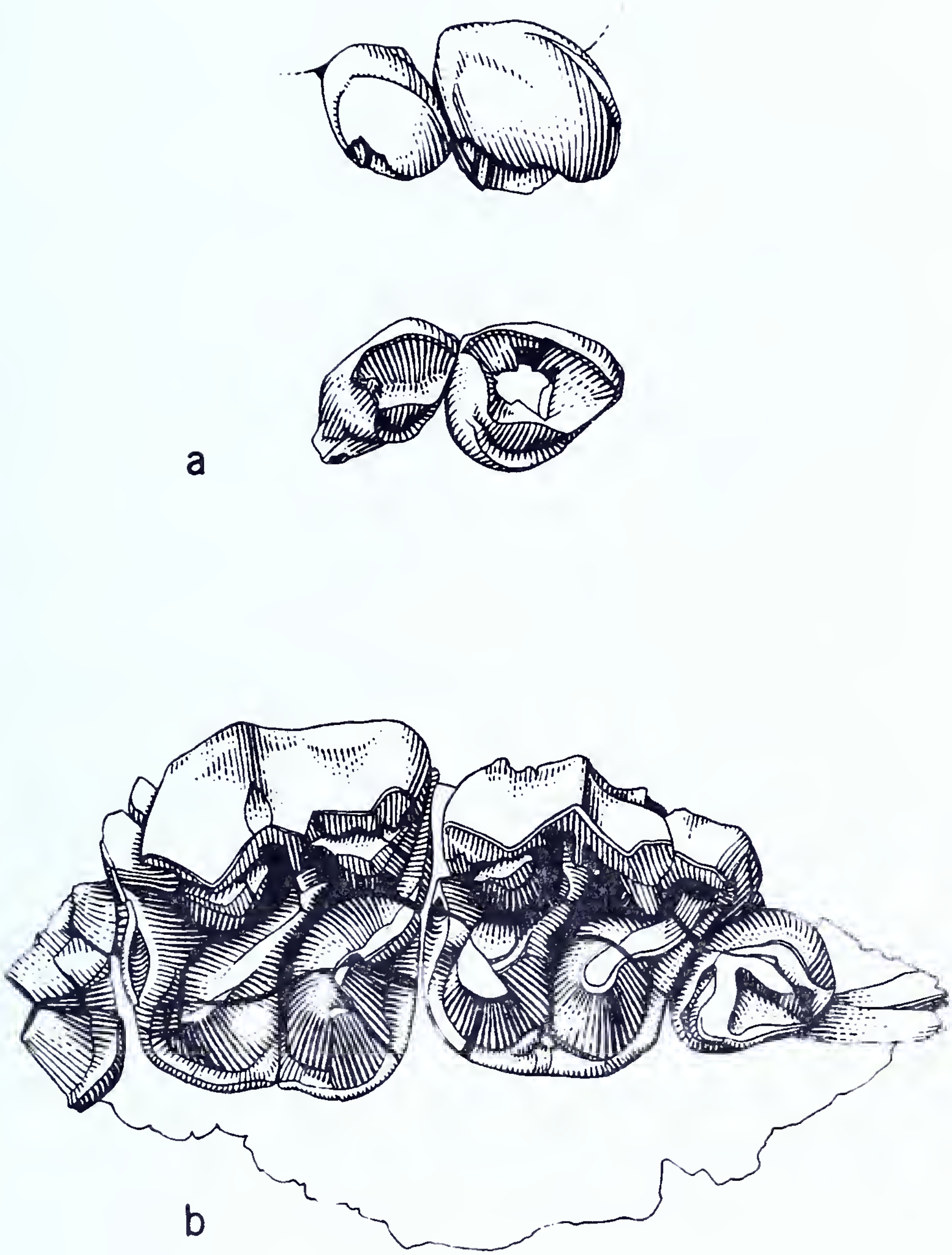

Figure 2. *Megahippus* cf. *M. matthewi*. UCMP 59271. *a*. Right I^2 and I^3. Above, lateral view; below, occlusal view. *b*. Fragment of right maxilla with P$^{1-3}$, part of P^4. X 1.

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PALEOBIOS

Contributions from the University of California
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No. 8 June 1, 1969

A MOLLUSCAN FAUNAL ASSEMBLAGE FROM THE ARCTURUS FORMATION, NEVADA

by

Thomas E. Yancey

no. 8

A MOLLUSCAN FAUNAL ASSEMBLAGE FROM THE ARCTURUS FORMATION, NEVADA

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INTRODUCTION

Middle Permian marine rocks of the Arcturus Formation in White Pine County, east central Nevada, contain an unusually diverse fauna, containing most of the non-reef marine faunal communities found in Pennsylvanian-Permian strata in the United States (Stevens, 1966). Brachiopods, corals, echinoderms, foraminifera, molluscs and bryozoans are all abundant, particularly the brachiopods and molluscs, providing one of the most complete marine faunal associations known in the far West. The upper part of the formation contains a dominantly molluscan fauna, contained in a distinctive lithology of shales and interbedded evaporites and limestones. Permian molluscan faunas are known from several areas in the western states, chiefly in Texas, Arizona, and the Wyoming-Idaho region, although even the better known of these are incompletely described, and none have been described from Nevada. Description of these molluscs is prompted by the need for information of molluscan species due to their increasingly important role in chorologic correlation of non-fusulinid bearing Permian strata.

Much diversity is apparent in molluscan faunas, with many molluscan communities known (Moore, 1964; Stevens, 1966), representing a range of environmental conditions. The faunal assemblage described here appears to represent a fossilized life assemblage, or biocoenose, and data is presented for the interpretation of the paleoecology of this assemblage. As some species (or related forms) characterize coeval faunas in other areas, their documentation should contribute to the analysis of adjacent communities.

ACKNOWLEDGEMENTS

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AGE AND LOCATION

The fossils from the Arcturus Formation were collected in 1957 by Dr. R. L. Langenheim and Dr. E. Wilson 25 miles southwest of Ely, Nevada, on the east side of Ward Mountain at an elevation of 7200 feet, approximately 1000 feet north of the south boundary and 150 feet west of the east boundary of Section 28, Township 16 North, Range 62 East (Mt. Diablo Base and Meridian). This is University of California Museum of Paleontology (UCMP) locality number B-6264. Precise stratigraphic position of the fossil assemblage was not determined when collected, but subsequent study indicates that UCMP B-6264 came from the upper part of the formation.

A Leonardian (Middle Permian) age is indicated by the joint occurrence of *Euphemitopsis subpapillosa* (White), *Straparollus* (*Leptomphalus*) *arcturus* Yancey n. sp., *Euphemites kingi* Yochelson and *Goniasma* cf. *G. geminocarinata* (Chronic). *Euphemitopsis subpapillosa* is known from the Yeso Formation in New Mexico and Epitaph Formation in Arizona (Yochelson, 1956), both Leonardian in age, and the Permian upper part of the Aubrey Group in Utah (White, 1876). Species of *Straparollus* (*Leptomphalus*) are known only from the middle Permian, and the closest relative to *S.* (*L.*) *arcturus* n. sp. is *S.* (*L.*) *micidus* Yochelson from the Leonardian Bone Spring Formation in Texas (Yochelson, 1956). *Euphemites kingi* previously was recorded only from the Bone Spring Formation (Yochelson, 1956). *Goniasma geminocarinata* is known only from the Alpha Member of the Kaibab Formation in Arizona, considered latest Leonardian by Chronic (1952).

In the vicinity of Ward Mountain, Permian molluscan faunal assemblages with euphemitine gastropods occur characteristically in the upper part of the Arcturus Formation (Wilson and Langenheim, 1962; Stevens, 1966). Brill (1963) placed this part of the Arcturus Formation in the lower Leonardian, and Wilson and Langenheim (1962) noted that it stratigraphically overlies rocks with Leonardian fusulinids. The age and characteristic occurrence of the faunal assemblage in the local stratigraphic column both indicate that UCMP B-6264 was collected from the upper part of the Arcturus Formation. Another molluscan sample from the same area, UCMP B-6207, containing poorly preserved specimens of *S.* (*L.*) *arcturus* n. sp., is from rocks overlying strata bearing Leonardian fusulinids.

COMPOSITION OF THE FAUNA

The fossils are silicified and were freed from limestone by etching with hydrochloric acid. Their preservation is usually good, but on many the outermost layer of shell is incomplete or missing. No indication of predepositional abrasion was noted; however many of the shells are fractured and crushed as a result of deformation of the rock.

Three species make up more than 90 percent of the individuals recovered from the acid residue: *Euphemitopsis subpapillosa* (most numerous), *Straparollus (Leptomphalus) arcturus* n. sp. and *Palaeonucula levatiformis* (Walcott). A hand-sized piece of this limestone contains tens of individuals of each of these species. Scattered among them are a few specimens of *Goniasma* cf. *G. geminocarinata*, *Goniasma* sp., *Euphemites kingi*, *Meekospira*? sp., many poorly preserved specimens of *Rimmyjimina* sp. and a few stellate crinoid collumnals. The small and delicate shells of *Rimmyjimina* sp. show a greater amount of post-burial crushing and incomplete silicification than the other species. One sees fewer individuals of *Rimmyjimina* sp. in the acid residue than on the weathered surfaces of the rock due to their poorer preservation, and they probably were an abundant constituent of the fauna.

The rock containing the fossils is a calcilutite with great admixture of shell material. Small shells are often oriented subparallel to bedding planes, but larger specimens show random orientation. Specimens of the bivalve *Palaeonucula* are usually articulated, and have a preferred orientation of the plane of commissure normal to the bedding. On weathered rock surfaces the gastropods show complete gradation of size from juveniles to adults, with juveniles being more abundant. Insoluble residues do not show this due to destruction of many of the small shells during acid etching.

PALEOECOLOGY

The random orientation of the larger shells and the thin bedding of the containing limestone indicate that the bottom, a shell rich substrate of fine mud, was not swept by strong currents. Presence of weak current action is indicated by the generally parallel orientation of the smaller shells to the bedding planes. Evidence that the shells were not transported after death are 1) the predominantly random orientation of larger specimens, 2) absence of predepositional damage to the shells, and 3) preservation of articulated valves of *Palaeonucula*.

Yachelson (1960) described and illustrated an assemblage of fossils from the Hueco Limestone of Wolfcampian age in New Mexico, United States National Museum (USNM) locality 712-b, which is similar to the assemblage from UCMP B-6264, and he presented evidence that it represents a portion of a fossil biocoenose. His criteria for this conclusion were the presence of a variety of species, random orientation of the shells, abundance of smaller shells as compared to larger shells and presence of only a few abraded shells.

The association at UCMP B-6264 shows very similar characters. In addition, some of the articulated valves of *Palaeonucula* are oriented normal to the bedding, which is the life position of modern nuculid bivalves such as *Nucula* (Morton, 1958). The above evidence indicates the preservation of a biocoenose at B-6264 in which the mobile epifauna dominants were *Straparollus* (*Leptomphalus*) and *Euphemitopsis*, whereas *Palaeonucula* and perhaps *Rimmyjimina* dominated the infauna. The gradation in size of *Straparollus* (*Leptomphalus*) and *Euphemitopsis* specimens and the association of many small individuals with large ones indicate a former biocoenose and not a mixed death assemblage. The presence of large numbers of diverse growth sizes of *Straparollus* (*Leptomphalus*) and *Euphemitopsis* on a mud substrate suggests their complete adaptation to the environment, perhaps as scavengers or detritus feeders. As Thorson (1957) demonstrated in the living faunas, clayey or muddy sediments are inhabited by detritus feeders or scavengers.

Yonge (1947) observed that modern aspidobranch gastropods (archeogastropods) live primarily on hard substrates. He based this conclusion on studies of the ctenidea and gill structures, showing that these gastropods cannot live for long periods in turbid water. The amount of turbidity in the water is the critical factor controlling the distribution of archeogastropods rather than the hardness of the substrate. The archeogastropods from UCMP B-6264 and USNM 712-b are embedded in a matrix of lithified calcareous mud containing large amounts of shell material. The mud substrate was probably firm rather than soft because of the considerable biologic activity occurring within it. Such biologic activity normally results in a binding of fine sediments into a firm consistency (Ginsburg, 1957). *Straparollus* (*Leptomphalus*) *arcturus* n. sp. and *Euphemitopsis subpapillosa* apparently flourished in relatively clear water on a firm lime-mud substrate.

Archeogastropods could inhabit substrates other than hard ones, because movement over a soft mud need not produce agitation of the bottom sediment if the gastropod has a foot that extends over an area much larger than the shell width. Some living naticid gastropods (e.g. Natica chemnitzii Pfeiffer) have a foot that extends several shell-widths beyond the aperture and they are able to crawl relatively rapidly over a very soft substrate without disturbing the mud or sinking into it. Likewise the bellerophontid gastropods, which have similar proportions of body chamber size to total shell size, may have had an equally extendable foot and could have inhabited any kind of substrate, hard or soft.

This faunal assemblage is similar to the euphemitid community described by Stevens (1966). Euphemitopsis, Straparollus (Leptomphalus) [identified as Straparollus (Euomphalus) by Stevens] and Palaeonucula, the most abundant constituents of UCMP B-6264, all occur in common with the euphemitid community. The occurrence of this community in predominantly non-calcareous rocks, association with strata containing evaporite deposits, and its close resemblance to modern faunas in brackish or hypersaline waters led Stevens to conclude that it had a tolerance for higher salinities and lived in shallow pools and bays in depths of four meters or less.

The euphemitid community at UCMP B-6264 occurs in an atypical rock for it (highly calcareous limestone), contains molluscan elements in common with other communities clearly not of hypersaline environments, and contains crinoid columnals. This indicates that the environment for UCMP B-6264 was at near normal salinity. The gastropod genus Goniasma is also present in the faunas of Chronic (1952) and Winters (1963) which, by their diversities and species content, were considered to be from waters of near normal salinity. The bivalve Rimmyjimina is also in common with Chronic's fauna. The euphemitid community described by Stevens is a hypersalinity tolerant community, while UCMP B-6264 appears to be a near normal salinity expression of this community.

SYSTEMATIC PALEONTOLOGY

Terminology used in the following systematic descriptions of gastropods follows the usage of Cox (1960) and Yochelson (1960). All types and figured specimens are deposited in the type collections of the University of California Museum of Paleontology.

no. 8

BIVALVIA

Superfamily NUCULACEA Gray, 1824
Family NUCULIDAE Gray, 1824
Genus PALAEONUCULA Quenstedt, 1930

Palaeanucula levatiformis (Walcott), 1884
Figures 18-20

Nucula levatiforme Walcott, 1884, U. S. Geol. Survey, Mon. 8, p. 241, pl. 22, fig. 1, 1a.
Palaeonucula levatiformis (Walcott), Chronic, 1952, Geol. Soc. Am. Bull. 63, p. 138, pl. 6, figs. 4-9.
Palaeonucula levatiformis (Walcott), Winters, 1963, Geol. Soc. Am. Mem. 89, p. 49, pl. 6, figs. 4-7b.

Hypodigm: About 50 specimens, juveniles and adults. Figured specimens are hypotypes UCMP 10130, UCMP 10131 and UCMP 10132.

Description: Small, subtriangular, averaging about as high as long, with beaks situated forward of center of hinge line; beaks in some specimens close to anterior margin of shell, close to midpoint in others; outline of shell variable, generally close to equilaterally triangular; well inflated with thickest part about one-third height below beaks; ornamentation consisting of many low concentric ribs, some individuals having a few irregular growth constrictions superimposed over these; lunule sharply defined and large, enclosing a flattened area below the beaks extending to ventral margins, with slight outward bulge midway between beaks and margins; taxodont dentition with about 10-11 anterior teeth and 6-7 posterior teeth; small ligament groove beneath beaks; individuals reaching 7 mm in height and 7 mm in length.

Discussion: Most of the specimens were individuals with articulated valves. These specimens compare well with the material described by Chronic (1952) and with material described by Winters (1963). The amount of variation in outline is even greater than that illustrated by Winters (1963), with the height-length ratio ranging from 1:1.5 to 1.5:1. Variation of other characters appear to be dependent on the changes in dimensions of the shell, and in no case are they as extreme as the height-length variations.

no. 8

Superfamily CARDITACEA Goldfuss, 1820
Family MYOCONCHIDAE Newell, 1957
Genus RIMMYJIMINA Chronic, 1952

Rimmyjimina sp.

Rimmyjimina Chronic, 1952, Geol. Soc. Am. Bull. 63, p. 148, pl. 9, figs. 7-11b.

Hypodigm: Five specimens.

Description: Shell small, ovoid; strong cardinal tooth definitely present in right valve; left valve appears to lack any strong tooth; cardinal margin gently convex, with very small beaks positioned slightly above hinge line; largest complete specimen 5 mm in length; incomplete specimens reach 10 mm in length.

Discussion: The specimens show the characteristic decrease in height toward the anterior end, the strongly produced anterior margin of *Rimmyjimina*, and the dentition appears to be the same as in Chronic's illustration of *Rimmyjimina*. Despite the strong resemblance to *Rimmyjimina arcula* Chronic, the Arcturus material is too fragmentary to refer it to that species.

GASTROPODA

Superfamily BELLEROPHONTACEA M'Coy, 1851
Family SINUITIDAE Dall, 1913
Subfamily EUPHEMITINAE Knight, 1956
Genus EUPHEMITES Warthin, 1930

Euphemites kingi Yochelson, 1960

Euphemites kingi Yochelson, 1960, Bull. Am. Mus. Nat. Hist., Vol. 119, Art. 4, p. 248, pl. 47, figs. 5-11.

Hypodigm: One complete specimen. Figured hypotype UCMP 10122.

Description: Shell laterally compressed, having an ovoid outline; aperture narrow, with distinct slit about 4 mm deep on outer lip; about 13 narrow, closely spaced lirae in aperture extending adaperturally about one-quarter of circumference of outer whorl where most lirae terminate, with a few fine lirae continuing for an additional half of whorl circumference; selenizone wide, covering one-quarter of the width of shell, and bordered by two indistinct lirae; lateral lips sickle-shaped; specimen 10 mm in width, 15 mm in diameter.

Discussion: The compressed form of the shell, and the number, form, and extent of the lirae are diagnostic for E. kingi. The available material appears identical to specimens described and illustrated by Yochelson.

Genus EUPHEMITOPSIS Yochelson, 1960

Euphemitopsis subpapillosa (White), 1876

Figures 9-13

Bellerophon carbonarius Cox, var. subpapillosa White, 1876, U. S. Geol. and Geog. Surv. Terr., Report on the Geol. of the Uinta Mts., p. 92.

Euphemites subpapillosa (White), Knight, 1953, in Cooper et al., Smithsonian Misc. Coll., Vol. 119, No. 2, p. 85, pl. 25A, fig. 6, not figs. 1-5, 7-8.

Euphemitopsis subpapillosa (White), Yochelson, 1960, Am. Mus. Nat. Hist. Bull. 119, Art. 4, p. 254, pl. 48, figs. 13-14.

Hypodigm: About 100 specimens. Figured specimens are hypotypes UCMP 10123-10126.

Description: Shell globose, tightly coiled, and approximately as wide as high; outer lip with wide and shallow sinus, cut by deep narrow slit; lateral lips strongly curved and sickle-shaped; selenizone wide in juvenile specimens, widening less than shell during growth, and is proportionally narrower in adult whorls; selenizone bordered by two narrow lirae that merge into rounded lirae extending into aperture; one short narrow lira is often present at center of selenizone on adult shells, limited in length to about one-third of circumference, and located directly opposite aperture, but extending neither to aperture nor to outer lip; about 14 lirae within aperture with lateral ones somewhat nodose; lirae quite narrow and sharp on young whorls, becoming more rounded and more nodose on later whorls; lirae within aperture change abruptly from sharp elevations to unconnected lines of nodes, becoming more nodose closer to aperture on later whorls; eight to ten lines of distinct nodes in widely spaced rows developed on large shells; nodes uniform in size and well developed, some aligned in secondary rows parallel to aperture; size ranging from tiny juveniles to adults 15 mm in width and diameter.

Discussion: In the original designation of this species, White included many similar forms from several localities, some of which Knight first illustrated in 1953. Of the specimens Knight illustrated only the lectotype fits the concept of the species as presently understood, and the other forms fit into species described since or still undescribed. Euphemitopsis subpapillosa includes forms in which the lirae extend out no more than one-half the circumference of the outer whorl where some of them break into small, sharp, well spaced nodes which are not connected by any vestige of a rib. These features are seen on the illustration of the lectotype. Knight described the lirae as few (8-12) and well spaced. Yochelson's (1960) illustrations of hypotypes are the first illustrations which show enough characters to distinguish E. subpapillosa from other species of Euphemitopsis.

The variation in Euphemitopsis (Knight, 1953; Yochelson, 1960) and the closely defined species within the genus prompt an examination of the variation in this sample of Euphemitopsis subpapillosa. The most significant variation is ontogenetic. This ontogeny involves a gradual increase in the number of nodes on the outer whorl, associated with a decrease in the length of the lirae. The density of the nodes varies little during growth, making this character a good one for specific determination. The size of the individual nodes increases slightly but not markedly with increasing shell size. The width of the selenizone is proportionally smaller on later whorls, and the shell proportions change, becoming wider on later whorls. Lirae are sharper in outline on young individuals, becoming more rounded on later whorls. The lira segment located in the center of the selenizone was seen only on mature specimens. Many of these ontogenetic variations are shared with other species of Euphemitopsis. Within the population described here, individuals of the same size show minor variations, mostly in the placement of individual nodes and in the presence of eight or ten rows of nodes. Designation of species on the basis of degree of noding appears to be a highly useful approach.

Superfamily EUOMPHALACEA de Koninck, 1881
Family EUOMPHALIDAE de Koninck, 1881
Genus STRAPAROLLUS de Montfort, 1810
Subgenus LEPTOMPHALUS Yochelson, 1956

Straparollus (Leptomphalus) arcturus Yancey, new species
Figures 1-8

Hypodigm: 65 specimens, from juveniles to gerontic adults. Designated types: holotype UCMP 10113, figured paratypes UCMP 10114-10116, and unfigured paratypes UCMP 10117-10121.

Description: Shell small, discoidal; spire depressed with apex lying close to or below median plane of outer whorls, in some individuals almost in line with the base of outer whorl; widely phaneromphalous, with umbilical angle between 150° and 180°; sutures shallow and slightly impressed on top and bottom; both young and mature whorls bilaterally symmetrical in cross section; whorl narrowest near suture, increasing slightly in inflation outward to angulations near outer edge of whorl; upper angulation strong and lower angulation weak; basal angulation intermediate in cross-section between a true angulation and a low spiral rib; whorls with evenly rounded distal face; top surface of whorl flat, basal surface flat or slightly rounded; shell wall thickens outward from angulations, forming a thicker shell wall distally; growth lines orthocline, or gently opistocyrt on later whorls, extending outward to angulations, there bending into sharply defined but shallow sinuses on both top and bottom of whorl; beyond sinuses growth lines curve forward to the periphery forming slightly projecting outer lip; upper lip of aperture produced slightly forward over lower lip; each successive whorl about 50 percent wider and 50 percent thicker than preceding whorl; reaches 12-14 mm in greatest diameter; no instance of node-formation was observed.

Discussion: The species is easily distinguished from all other American discoid species of Straparollus by the combination of rounded whorls and positioning of apex of spire at or below the median plane of the shell. The hyperstropic coiling of this species is unique in Straparollus (Leptomphalus). It varies from definitely hyperstrophic to truly bilaterally symmetrical, with most individuals being slightly hyperstrophic. The growth lines are symmetrical on top and bottom of the whorl, with a sinus of equal size and magnitude on both angulations. In cross section the whorl profile has an elongated pentagonal form, but owing to thickening of the shell wall at the angulations, the internal shape of the whorl has a more rounded form. The thickened shell wall on the distal face of the whorl is perhaps a feature to be expected in other species of the subgenus. In the sample examined a very thin outer shell layer is often exfoliated and the suture appears deeper than normal.

The juvenile whorls are nearly round, with weak angulations, and they only gradually acquire the features that distinguish the adult whorls. By the third whorl the basic pentagonal outline is discernible. Large specimens are 12-14 mm in diameter and have five or six whorls, the thickness of the outer whorls reaching 4 mm. The protoconch consists of a rounded closure to the first whorl, in some specimens consisting of a chamber slightly larger than the first whorl. It is inconspicuous and lies entirely within the plane of the first whorl.

The only other described American species assigned to the subgenus *Leptomphalus* is *Straparollus (Leptomphalus) micidus* Yochelson, likewise known from silicified material. *S. (L.) arcturus* differs from *S. (L.) micidus* in having the apical whorls below the median plane, in the distal whorl-face being rounded as opposed to the slight shelving of *S. (L.) micidus* (see Yochelson, 1956), and in having stronger angulations, both on top and bottom. The two species appear to be closely related. The presence of a sinus in the upper angulation of *S. (L.) micidus* is to be expected, but whether it has one on the base needs to be determined.

The feature showing the greatest variation is the positioning of the apical whorls. There are extremes of placement from slightly above the median plane of the shell to almost as low as the lower surface of the outer whorl. The predominant position is distinctly below the median plane, resulting in an imperfect bilateral symmetry. Width of the initial apical whorl is as much as 25 percent of the width of the adult whorl. Older whorls often show a tendency to depart from earlier coiling symmetries and begin to coil downward.

Other characters show minor variation. The lower angulations are usually directly below the upper angulations, although in a few individuals they vary slightly from this alignment. The lower whorl surface is somewhat rounded inward from the angulation and the position of the basal angulation influences the amount of rounding, producing a flattened appearance if it is located inward from its normal position, and a more rounded appearance if it is placed outward. The growth lines may show minor variation from an orthocline position on the later whorls. This was noted on the whorls of four of the larger shells, three having opisthocyrt growth lines, and one with prosocyrt growth lines. This deviation from orthocline form appears to be a character of old age.

It is apparent in the many species of the subgenus that there is a great diversity of form within *Straparollus (Leptomphalus)* and that three different subgroupings can be distinguished within it. The North American species *S. (L.) arcturus* and *S. (L.) micidus* constitute the typological subgroup; that is, the one including the type of the subgenus. Another subgroup can be distinguished in the Asian species, characterized by *S. (L.) kweitingensis* (Graubau) and *S. (L.) pusillus* (Waagen). In these species the whorls enlarge rapidly in height and width, with each succeeding whorl about twice as wide and thick as its predecessor. A large body whorl gives this subgroup a distinctly different appearance. Coiling within this subgroup is exactly bilaterally symmetrical. A third subgroup is represented by the German species *S. (L.) discomphalus* (Dietz) and S. (L.) rennstiegensis (Dietz). They have a discoid shape with the adult body whorl abruptly coiling downward out of the earlier plane of coiling so that it does not cover all of the preceding whorl and instead projects below it. The growth line on the upper face of the whorl is strongly opisthocyrt with a large sinus close to the suture. Thus three subgroups are fairly distinct, and it seems certain that within each subgroup the species are closely related phyletically. There are not enough species known to determine the full extent of the subgroups, and their complex relation to Straparollus (Euomphalus) needs clarification. The gradation in form from species of Straparollus (Leptomphalus) to species of Straparollus (Euomphalus) indicates the possibility of a polyphyletic origin for Straparollus (Leptomphalus) as currently defined, with each subgroup representing a different lineage.

Several species intermediate in form between the large North American euomphalids and the North American leptomphalids form a heterogeneous complex whose members have few affinities to one another. None of these species are truly transitional between the euomphalids and leptomphalids. They each have depressed apical whorls, which suggests that depression of the apical whorls was a trend occurring in a large complex of unrelated or distantly related species, which in turn gave rise to the bilaterally symmetrical forms. Such bilaterally symmetrical forms could have arisen independently from several groups, and the existence of several subgroups of species currently assigned to Straparollus (Leptomphalus) is suggestive of such an origin.

Superfamily MURCHISONIACEA Koken, 1896
Family MURCHISONIIDAE Koken, 1896
Genus GONIASMA Tomlin, 1930

Goniasma cf. G. geminocarinata (Chronic), 1952
Figure 16

Murchisonia geminocarinata Chronic, 1952, Geol. Soc. Am. Bull. 63, p. 123, pl. 4, figs. 12-14.

Goniasma geminocarinata (Chronic), Batten, 1964, Am. Mus. Novitates No. 2165, p. 14, figs. 16-18.

Hypodigm: Five incomplete specimens. Figured specimen is hypotype UCMP 10128.

Description: Shell tall, high spired, small, with as many as ten or more whorls; whorls very short, almost twice as wide as high, with slightly impressed sutures; aperture not preserved; succeeding whorls appressed to a spiral rib on the basal portion of preceding whorl; slight shoulder developed immediately below the suture; whorl profile concave from below suture to upper edge of the selenizone, and carrying several fine spiral ribs; selenizone contained between two closely spaced spiral carinae after the 4th whorl, the lower carina projecting farther than the upper one on young whorls of less than 1.7 mm in diameter and the upper one projecting farther than the lower one on larger whorls; no evidence of node formation on the selenizone on whorls up to 2.2 mm in diameter; below the selenizone the whorl profile is sharply concave, bearing a few fine spiral ribs, and one prominant spiral rib just above the suture; selenizone located regularly at two-thirds the whorl height below suture; growth lines start normal to suture then curve backwards into the selenizone; growth lines below selenizone unknown; height of figured specimen 5.65 mm, and width of largest whorl 2.2 mm; incomplete unfigured specimens reach a maximum whorl diameter of 3.5 mm.

<ins>Discussion:</ins> The specimens are morphologically close to <ins>Goniasma geminocarinata</ins>, particularly juvenile specimens, as described and figured by Chronic, especially in details of the whorl profile and ribbing. Juvenile portions of the shell differ from adult portions, the former having a smaller spire angle and having the selenizone bordered by two carinae which are not noded until the whorl diameter reaches 2-3 mm (measurement determined from illustrations by Chronic). The spire angle on hypotype UCMP 10128 is 13°, almost identical to that of fig. 12 of Chronic of a juvenile specimen. The larger specimens that Chronic illustrated also show the juvenile portions of the shell to be higher spired than the adult portions. Hypotype 10128, with whorls up to 2.2 mm in diameter, does not possess nodes on the selenizone, and whorls 3.5 mm in diameter on other fragmentary specimens lack nodes. The lack of nodes on whorls of this diameter is not characteristic of the type of <ins>G. geminocarinata</ins>.

The number of whorls on the juvenile portions of the shell, at least 10, is greater than recognized by Chronic or Batten. The smallest three or four preserved whorls on hypotype 10128 have a larger spire angle, approaching 30°, than that of the whole specimen. The development of the carinae bordering the selenizone is complex. On the earliest whorls a single carina is present with a secondary and smaller rib appearing above the main rib on whorls of about 1.2 mm diameter. The upper carina becomes strong, equals, then surpasses the lower one in size. On whorls larger than 1.8 mm diameter (to 3.5 mm), the upper carina is larger than the lower.

The major difference between these specimens and the types of G. geminocarinata is the absence of nodes on the selenizone on whorls of 2-4 mm diameter. The strongly developed upper carina may also be a significant character. The available specimens are juveniles, and larger specimens must be obtained to determine if these characters continue into larger whorls.

Goniasma sp.

Figure 17

Hypodigm: One incomplete specimen. Hypotype UCMP 10129.
Description: Tall, high spired, small, with four whorls; apical whorls missing; whorls, including body whorl, very short and almost twice as wide as high; sutures slightly impressed; aperture wedge-shaped, with rudimentary canal; inner lip of aperture with a sharp angulation of about 130° to 140° formed by the sloping basal surface of adjacent whorl and vertical columella; siphonal canal rudimentary, consisting of a simple angulation between inner and outer lips; succeeding whorls appressed to a spiral rib on the basal portion of preceding whorl; growth lines unknown; slight shoulder immediately below suture; whorl profile seemingly even from suture to upper edge of selenizone, flattens across a wide carina, then is inclined toward suture; selenizone contained in a wide, smooth, flat carina; a spiral rib present just above suture; base of body whorl with a few strong spiral ribs; height 4.80 mm; greatest diameter 2.5 mm; spire angle 17°.
Discussion: This specimen differs from those assigned to Goniasma geminocarinata (Chronic) by the large and blunt carina, with a flat, smooth outer surface. The carina (containing the selenizone) is wider than in G. geminocarinata. On whorls of equal diameter with those on specimens of G. cf. G. geminocarinata, there is no indication of double carinae. The largest whorl (about 2.5 mm diameter) shows a slight irregularity on the carina suggestive of undulations.

Superfamily SUBULITACEA Lindstrom, 1884
Family MEEKOSPIRIDAE Knight, 1956
Genus MEEKOSPIRA Ulrich, 1897

Meekospira ? sp.

Figures 14-15

Hypodigm: One crushed but complete specimen. Hypotype UCMP 10127.

Description: Shell high spired; six inflated, rounded whorls, body whorl a little larger than earlier whorls; shell very thin and covered with many low, broad, spiral ribs separated by incised spiral lirae; sutures deeply impressed; aperture ovoid, with the lower part of inner lip reflexed outward; growth lines unknown; 7.5 mm in height, 3.2 mm in greatest whorl diameter.

Discussion: This specimen has the low spire angle and relatively small body whorl typical of species of *Meekospira*, and resembles *Meekospira knighti* Winters closely in whorl proportions, spire angle, and shell outline, but it is dissimilar in its greater whorl inflation and its possession of spiral ribs. These last two characters suggest a relation to the Carboniferous genus *Aclisina*, but no trace of a selenizone is apparent in the aperture of the specimen. Furthermore, no genera in the family Meekospiridae are known to include species with ornament on the shell. Several possibilities exist for the classification of this specimen: it may be an ornamented species of the genus *Meekospira* (requiring an emendation of the genus definition), it may be related to *Aclisina*, or it belongs in a separate undescribed, ornamented meekospirid genus. The ornamentation is very inconspicuous and only because the quality of preservation is excellent can it be seen. Observed lack of ornamentation on species of *Meekospira* could well be due to a lack of sufficiently well preserved material for the determination of fine details.

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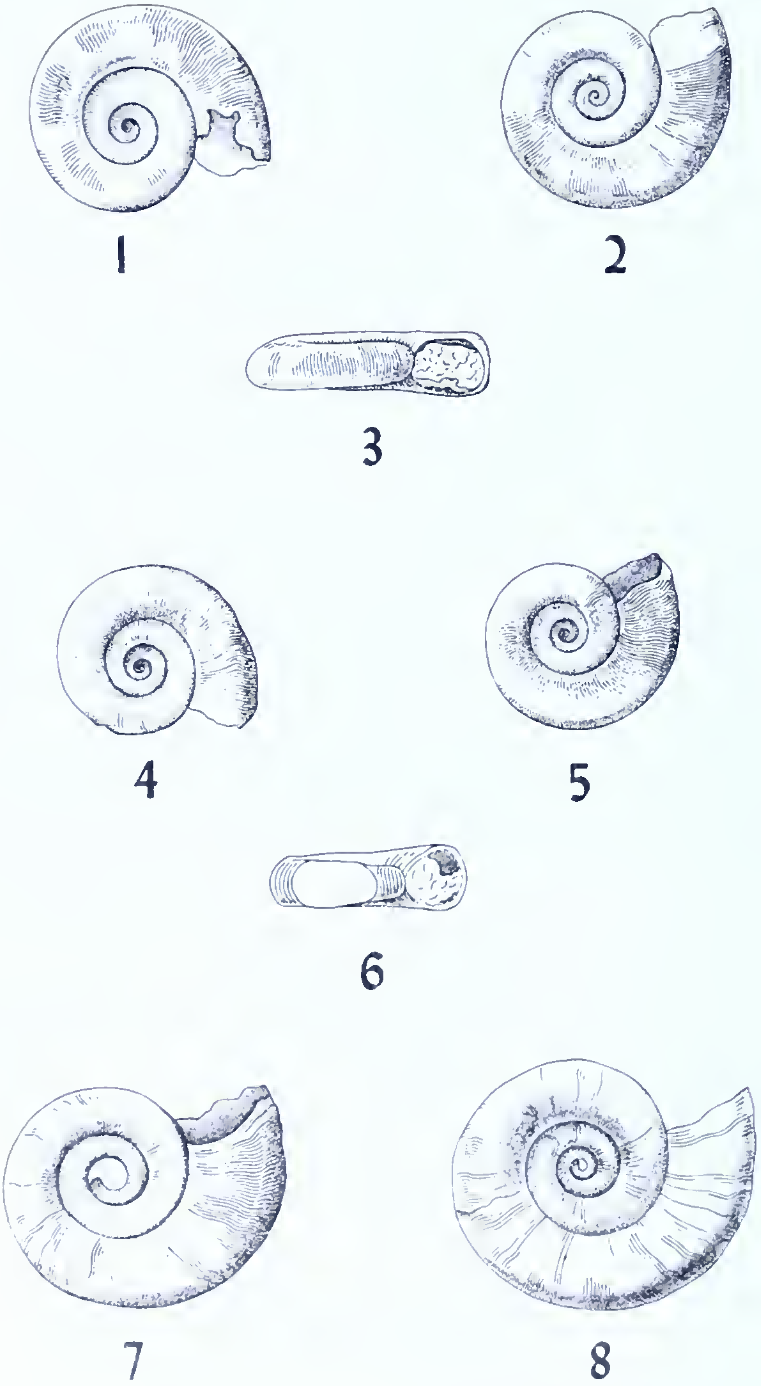

Straparollus (Leptomphalus) arcturus Yancey n. sp.

Figs. 1-3. Holotype, top, bottom and apertural views, X 3, UCMP 10113.
Figs. 4-6. Paratype, top, bottom and apertural views, X 3, UCMP 10114.
Fig. 7. Paratype, bottom view, X 3, UCMP 10115.
Fig. 8. Paratype, bottom view, X 3, UCMP 10116.

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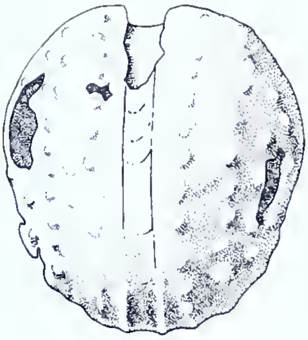

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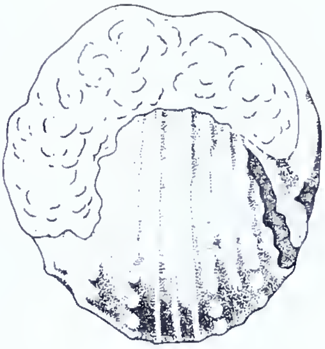

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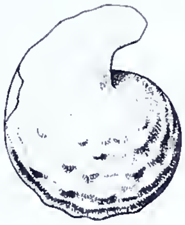

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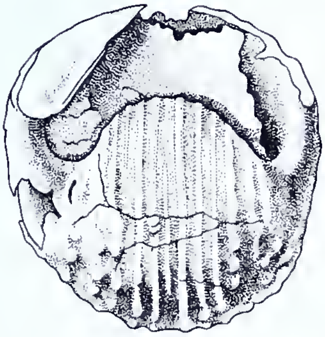

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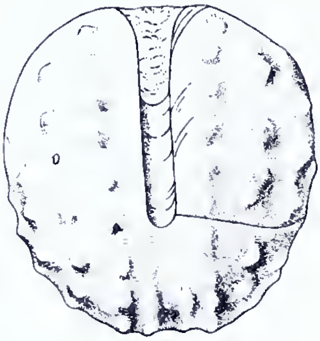

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Euphemitopsis subpapillosa (White)

Figs. 9-10. Hypotype, adapertural and apertural views, X 3, UCMP 10123.
Fig. 11. Hypotype, lateral view, juvenile specimen, X 3, UCMP 10124.
Fig. 12. Hypotype, apertural view, X 3, UCMP 10125.
Fig. 13. Hypotype, adapertural view, X 3, UCMP 10126.

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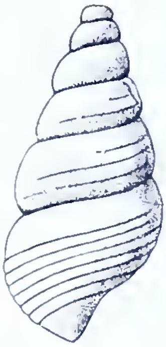

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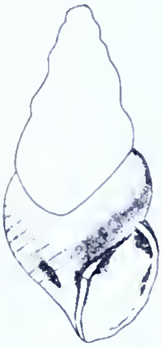

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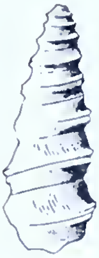

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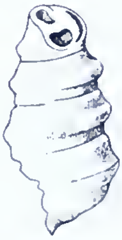

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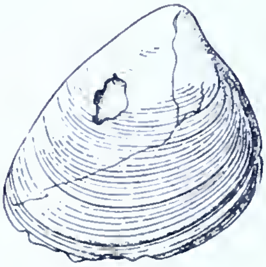

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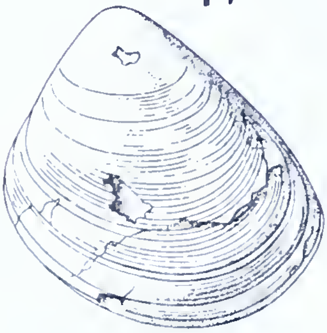

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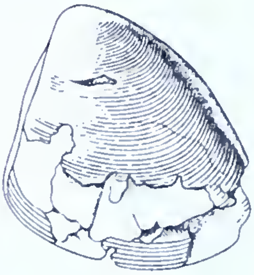

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Meekospira ? sp.

Figs. 14-15. Hypotype, adapertural and apertural views, X 6, UCMP 10127.

Goniasma cf. G. geminocarinata (Chronic)

Fig. 16. Hypotype, X 6, UCMP 10128.

Goniasma sp.

Fig. 17. Hypotype, X 6, UCMP 10129.

Palaeonucula levatiformis (Walcott)

Fig. 18. Hypotype, exterior of right valve, X 6, UCMP 10130.

Fig. 19. Hypotype, exterior of left valve, X 6, UCMP 10131.

Fig. 20. Hypotype, exterior of left valve, X 6, UCMP 10132.

no. 8

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No. 9 December 1, 1969

AN INVESTIGATION OF THE DIATOMS FROM FOUR TERTIARY LAKE BED DEPOSITS IN WESTERN NEVADA

by

Gunilla Smedman

no. 9

AN INVESTIGATION OF THE DIATOMS FROM FOUR TERTIARY LAKE BED DEPOSITS IN WESTERN NEVADA

BY GUNILLA SMEDMAN

In an attempt to evaluate the development of the diatom flora for its potential use in stratigraphic correlations, samples from a succession of late Tertiary lake bed deposits in western Nevada (see index map, Fig. 1) were investigated qualitatively and quantitatively. To meet the requirements for such an investigation, the stratigraphy should be well defined and dated by mammals, leaves, or potassium-argon dating; the ecological conditions postulated for the different localities should also be as similar as possible. These requirements are fulfilled for the sections at Aldrich Station and Stewart Valley. However, the age of the Buffalo Canyon and Ione Road localities is more uncertain. At all four localities samples were collected through the section from the oldest part to the youngest, with special interest shown wherever changes in the sedimentation occurred.

Each sample was treated with 10% hydrogen peroxide in a boiling water bath for 5-15 minutes. The mounting medium was Caedax. Approximately 200 diatoms were analyzed in each sample with a Zeiss photomicroscope under X800 magnification.

DISCUSSION OF DIATOMS BY LOCALITY

Aldrich Station Locality. The Aldrich Station Formation has been mapped and described by D. I. Axelrod (1956), and determined to consist of fluvio-lacustrine deposits of siliceous shales, diatomaceous shales, siltstone, sandstone and volcanic pebble beds formed during the late Barstovian to the early Clarendonian. Samples for diatom analyses (table 1) were collected from units A 2 through A 5 (see map, Fig. 2, of Axelrod, 1956). Units A 2, A 4 and A 5 are lacustrine, and unit A 3 is fluviatile in origin. Three samples were examined from A 2 but no diatoms were found. In the five samples analyzed from A 3, diatoms were found only in the upper part, whereas the five samples from A 5 all contained diatoms. Samples in the lower and middle parts of the section comprising unit A 5 were analyzed in detail. One analysis was also made of the lower Pliocene leaf locality at Lewis Coal Mine (locality P3917, Fig. 2, Axelrod, 1956).

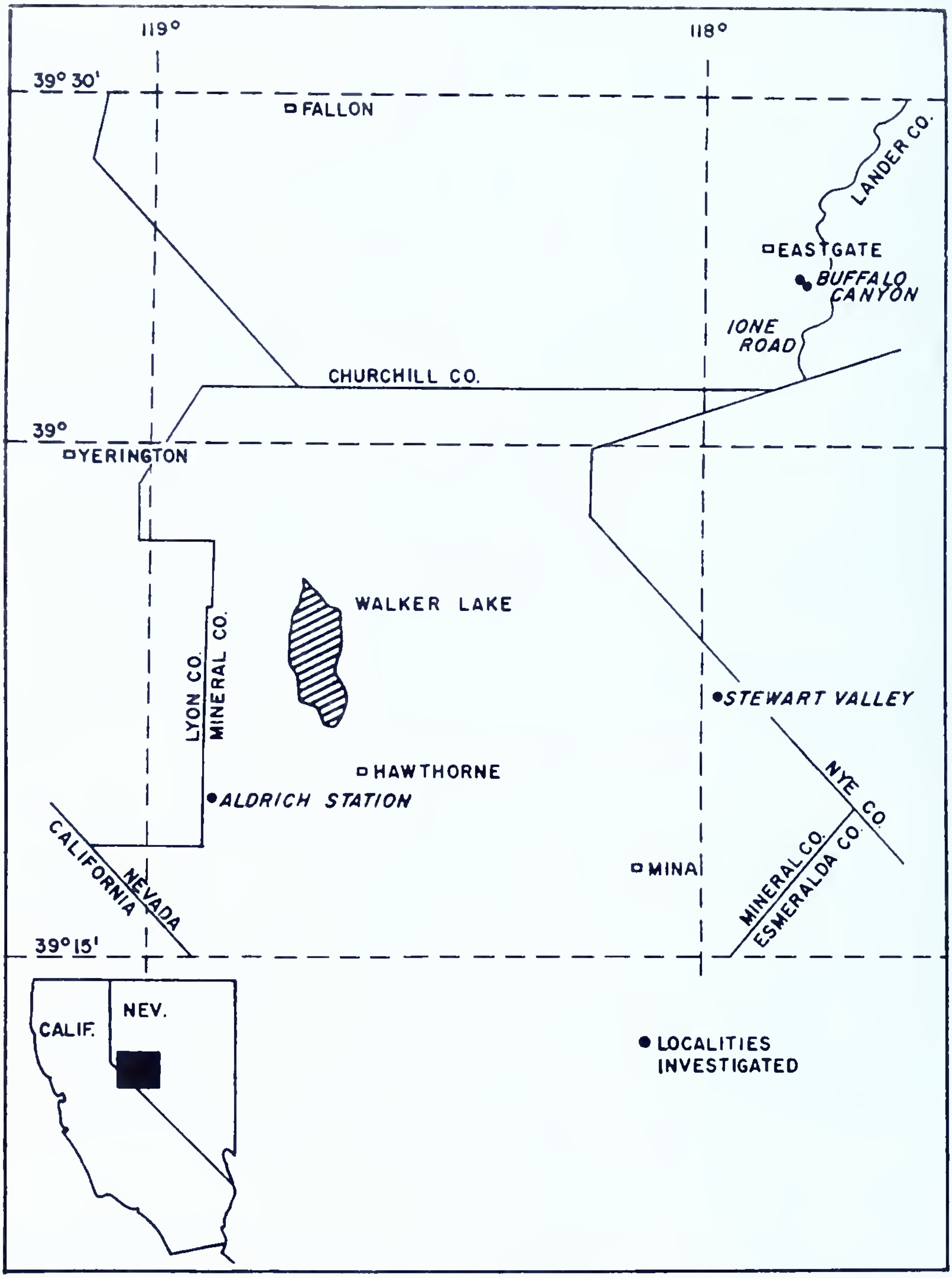


Figure 1. Index map.

Diatoms of Aldrich Station are represented by 28 different species (table 1) all belonging to a characteristic fresh water flora. Although all species are still extant, some, such as Coscinodiscus lacustris Grunow and Melosira granulata (Ehrenberg) Ralfs, are now very rare in this area. Five species are present at the first appearance of diatoms in the upper part of A 3. This lower part of the total section contains predominantly centrales such as Melosira and one species of Coscinodiscus, viz. C. lacustris which is euryhaline. The latter is found along coasts, river mouths, lakes with high salinity, but also in fresh water lakes with normal salinity. However, higher in the section but still in the upper Miocene (Units A 4 and A 5), the high values of M. granulata and the decreasing percentage of M. islandica Müller, which is a coldwater form, may indicate a warmer period and a clear alkaline lake. M. granulata disappears in the Early Pliocene (Unit C 1).

The flora of Aldrich Station consists mostly of planktonic and epiphytic diatoms; only two benthonic species have been found: Nitzschia amphibia Grunow and Stauroneis phoenicentron Ehrenberg.

Buffalo Canyon Locality. Six samples were analyzed in the diatomite section at Buffalo Canyon situated about eight miles southeast of Eastgate, Nevada, on U. S. Highway 50. The formation is unnamed, but the geology of the area is being studied by D. I. Axelrod. The leaf flora near the base of the section is mentioned by Axelrod (1956) who considered the flora to be of Barstovian age. Axelrod (per. comm. Feb. 1968) has since obtained a potassium argon date of about 16 million years B.P. for the tuffs just above the leaf beds. In terms of North American Land Mammal Chronology this places the lower part of the section in the later Hemingfordian or earliest Barstovian (=Middle Miocene).

The first sample (P 1, table 2) was collected at the leaf locality near the base of the section, and the last one (P 6) in a bituminous layer which terminates the lake bed deposition. Twenty-nine species of fourteen genera were found. Most species belong to an ordinary lake flora. Two exceptions are Achnanthes hauckiana Grunow and Synedra tabulata (Agardh) Kützing which live in brackish environments near shores and in river mouths. Both are, however, euryhaline and thus have no specific salinity requirements. Moreover, both are known to occur in lakes with high salinity, and at Buffalo Canyon only a small number appear in two different horizons. Since the other diatoms are ordinary fresh water inhabitants, A. hauckiana and S. tabulata might have had less specific requirements in the past.

no. 9

The flora of the base of the section contains a very high percentage of centrales such as *Melosira* and includes one species of *Coscinodiscus* which has been identified as being a new species, *C. nevadensis* (Fig. 3). *M. islandica* dominates the flora, but *M. distans* Müller is also very common. In the middle part of the section different pennales species of *Cymbella* appear, and *M. granulata* becomes the most common diatom. In the upper part of the section the presence of benthonic forms such as *Pinnularia* and *Navicula*, and of epiphytes of the genus *Gomphonema*, indicate a decreased water depth and filling of the lake with sediment. The diatoms of Buffalo Canyon lived in an eutrophic alkaline lake.

Ione Road Locality. The Ione Road section (table 3) is situated about 0.7 miles northwest of Buffalo Canyon. It consists mainly of diatomite, tuff, and claystone. It was deposited in the same lake basin as the Buffalo Canyon section and is stratigraphically above the Buffalo Canyon section with approximately 500 feet of volcanic material separating the two localities. The lowest part of the Ione Road section consists of lignitic tuffaceous clay and is terminated by a lignitic layer. The similarity in the diatom flora indicates a close relationship between the two localities.

Four samples were collected from this section. The oldest one (P 1), the lignitic tuffaceous clay, did not contain diatoms. In the other three samples, ten genera and 20 species were found. Of the 20 species, 14 occur at Buffalo Canyon. The additional six at Ione Road are *Cymbella gastroides* Kützing, *Fragilaria leptostauron* (Ehrenberg) Hustedt, *Navicula cincta* (Ehrenberg) Kützing, *Nitzschia linearis* Grunow, and *Synedra pulchella* (Ralfs) Kützing.

The Ione Road locality, however, is somewhat different from the other three localities. *M. granulata* is nonexistent at this locality whereas it is one of the predominant species in the others. The only centrales which has been found at this locality is *M. distans* var. *africana* Müller which also occurs in the Buffalo Canyon section but in much smaller numbers. Accordingly, planktons are present at a much lower percentage in the Ione Road section than in the other sections, and epiphytes predominate. A possible explanation may be that the lake beds at this locality were deposited near the shore in shallow water. *S. pulchella* and *S. tabulata*, which are common in brackish water, were found. However, both are euryhaline and may therefore survive in a lake with a moderately low salinity.

Composition of the diatom flora indicates, as in Buffalo Canyon, an eutrophic (bodies of water rich in mineral nutrients and organic materials, therefore productive) alkaline lake, suggesting a close relationship between the two localities in time as well as environment.

Stewart Valley Locality. The last section studied was the diatomite in Stewart Valley (table 4) belonging to beds commonly referred to the Esmeralda Formation. The geology and exact locality northwest of Cedar Mountain is described by Mawby (1965, unpublished PhD dissertation, University of California, Berkeley). The diatomite is lithologic unit Number 8 as recognized by Mawby. The next unit above, termed Clarendonian by its mammals, has been determined by a potassium-argon date to be 11.5 million years before Present (KA577, Evernden et al., 1964). The diatomite is probably Barstovian.

Samples representing the whole diatomite section were studied, and analyses were performed where any changes in the sedimentation or the flora were suspected. This section has a total of 13 genera and 22 species. At two horizons a new species of *Gomphonema* was identified which is here named *G. leifum* (Fig. 4).

All Stewart Valley diatoms belong to fresh-water forms except *Coscinodiscus lacustris*, which also occurs at Aldrich Station. In both sections it appears for only a short time. *Achnanthes saxonica* (de Brébisson) Grunow, which is a rather uncommon species, is found in one horizon.

COMPARISON OF THE DIATOM FLORAS

The Stewart Valley and Aldrich Station sections are approximately equivalent in age (Late Miocene), and there are several resemblances in their diatom floras. Thirteen of the species at Stewart Valley are also present at Aldrich Station. Predominant among centrales is *M. granulata*, which reaches about 900% (counts per 1000) and 760% at Stewart Valley, and thus it is the most common diatom in the two sections. Also present at both localities is another of the centrales, *C. lacustris*. Pennales common to both localities are *Achnanthes lanceolata* (de Brébisson) Grunow, *Cocconeis placentula* Ehrenberg, *Fragilaria brevistriata* Grunow, *F. construens* (Ehrenberg) Grunow, *F. pinnata* Ehrenberg, and *F. virenscens* (Ehrenberg) Grunow. One subspecies, *F. pinnata* var. *lancettula* (Schumann) Hustedt, is present in three of the six horizons at Aldrich Station and throughout the Stewart Valley section. In addition to the earlier mentioned *M. granulata*, two common *Melosira* species, *M. islandica* and *M. italica* (Ehrenberg) Kützing, are present at the two localities.

The vast majority of diatoms of Stewart Valley indicate alkaline eutrophic water. However, two diatoms, Cyclotella stelligera Cleve et Grunow and Diploneis finnica (Ehrenberg) Cleve, are considered to prefer oligotrophic (ponds or lakes that are low in content of basic nutritive substances for plants, lacking a distinct stratification of dissolved oxygen in summer or winter)-dystrophic (a type of lake or pond which contains brown water with much humic material in solution and with a small bottom fauna characterized by pronounced oxygen consumption) environments.

Whether the 13 species which are present at Stewart Valley as well as Aldrich Station have any significance for age determination is difficult to ascertain because all of them still exist. Because the environments of the two localities were the same, their diatom floras also show great similarities even if they did not correspond in time.

CONCLUSIONS

In order to use fresh-water diatoms for accurate stratigraphic correlations, a more extensive investigation is required, especially since most of the species are rather camman and still extant. Two new species, Coscinodiscus nevadensis and G. leifum, occur at only one locality and are thus of little stratigraphic value at this time.

A summary of the different diatoms present during Middle and Late Miocene and Early Pliacene is shown in Figure 2. Samples older than Middle Miocene do not contain any diatoms in the investigated area. A more comprehensive investigation of Early Miocene deposits however would reveal their presence, especially because the oldest diatoms found in the Middle Miocene are well developed and advanced. The general trend fram centrales in the Middle Miacene ta pennales in the Early Pliocene may be significant in the development of the flora. C. nevadensis occurs in Middle Miocene and G. leifum in Late Miocene deposits, and as mentioned earlier, they have very shart ranges. Two rather uncommon diatoms are C. lacustris, found throughout the Late Miacene, and A. saxonica, also found only in the Late Miocene. M. granulata, which is ane of the index fassils, appears throughaut the Middle and Late Miocene. Other investigations of Middle Miocene diatams (Lahman, 1936; Krasske, 1934; van Landingham, 1964) have also reparted high values of M. granulata, and thus it once had a much wider range than at present. In the Early Pliocene at Aldrich Station, M. granulata is absent. This is also the case far the Middle Miocene sample of lone Road, but here the absence af M. granulata is the result of local conditions. Thus, low values of *M. granulata* do not necessarily exclude Miocene age.

Correlations with earlier investigations on Miocene fresh-water diatoms in western United States (Lohman, 1936 and 1961; van Landingham, 1964) are questionable, especially because one report (Lohman, 1961) does not describe the short-ranging extinct species. Thus, further and more detailed investigations are required for evaluating the significance of diatoms in stratigraphic correlations over large areas.

SYSTEMATIC SECTION

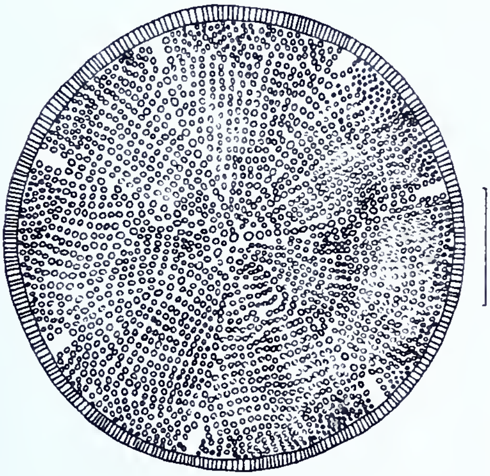


Fig. 3. (scale = 10 microns)

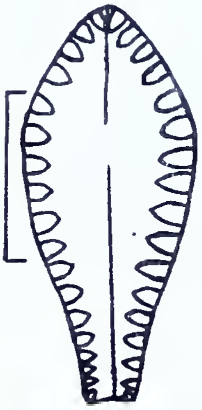


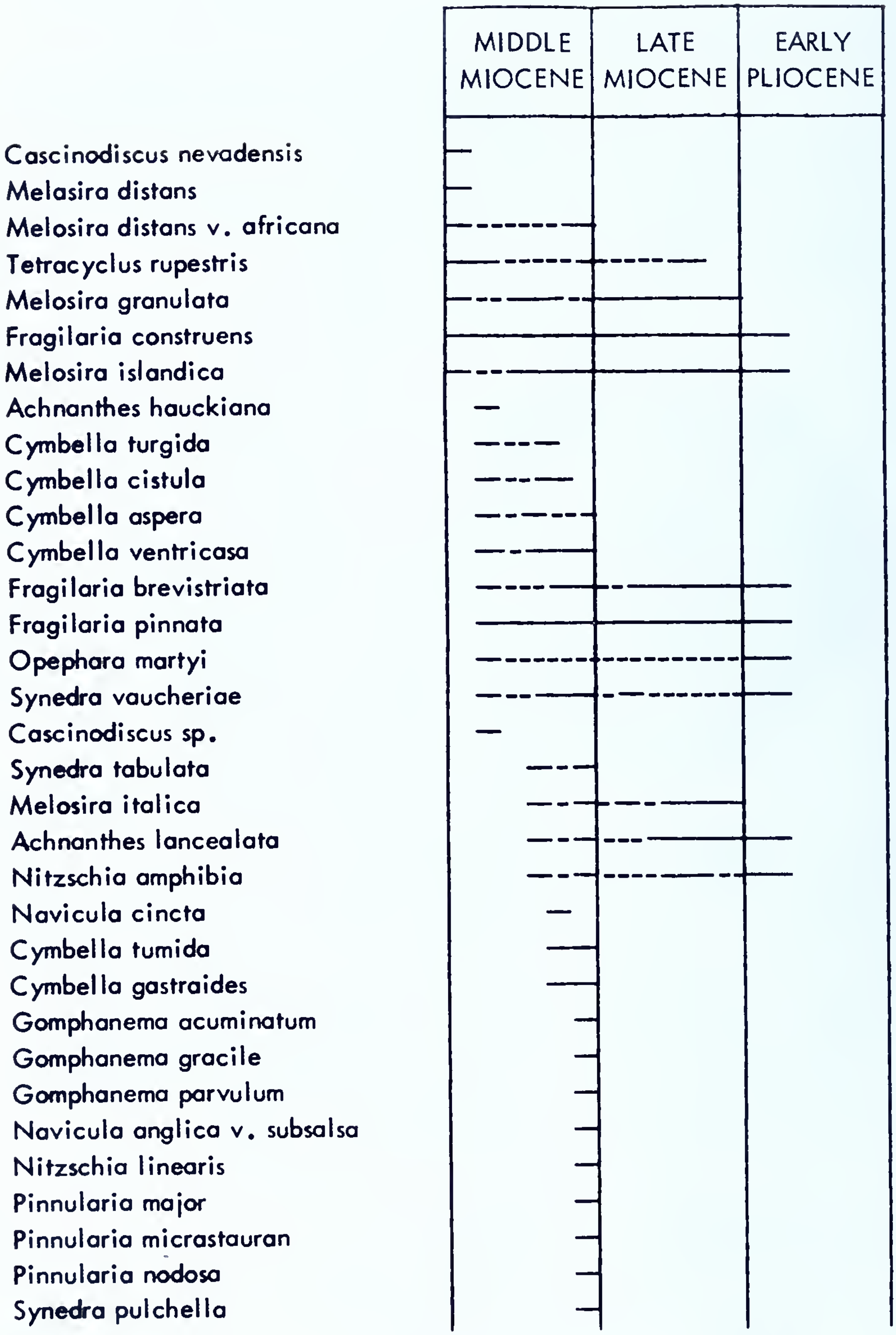
Fig. 4. (scale = 10 microns)

Coscinodiscus nevadensis n. sp. Fig. 3.

Samples from Buffalo Canyon section P1.
Dimensions: Diameter 35–80 microns; areolae 12 in 10 microns; marginal striae 16–20 in 10 microns.
Center is a small hyalin area. Valva is divided into 5–7 sections by dotted rows which end 1/3 from the margin with a hyalin spot. The radial rows within the section are regular to 1/3 from the margin where they break up into more or less irregular punctuation. The margin is striated.

Gomphonema leifum n. sp. Fig. 4.

Samples from Stewart Valley section P10 and P13.
Dimensions: Length about 24 microns; width about 9 microns; striae 12 in 10 microns.
Valva breadth lanceolate with cuneate head. Axial aria wide occupying half the valva. Striae radial.


MIDDLE MIOCENE
LATE MIOCENE
EARLY PLIOCENE
Cascinodiscus nevadensis
Melasira distans
Melosira distans v. africana
Tetracyclus rupestris
Melosira granulata
Fragilaria construens
Melosira islandica
Achnanthes hauckiana
Cymbella turgida
Cymbella cistula
Cymbella aspera
Cymbella ventricasa
Fragilaria brevistriata
Fragilaria pinnata
Opephara martyi
Synedra vaucheriae
Cascinodiscus sp.
Synedra tabulata
Melosira italica
Achnanthes lancealata
Nitzschia amphibia
Navicula cincta
Cymbella tumida
Cymbella gastraides
Gomphanema acuminatum
Gomphanema gracile
Gomphanema parvulum
Navicula anglica v. subsalsa
Nitzschia linearis
Pinnularia major
Pinnularia micrastauran
Pinnularia nodosa
Synedra pulchella

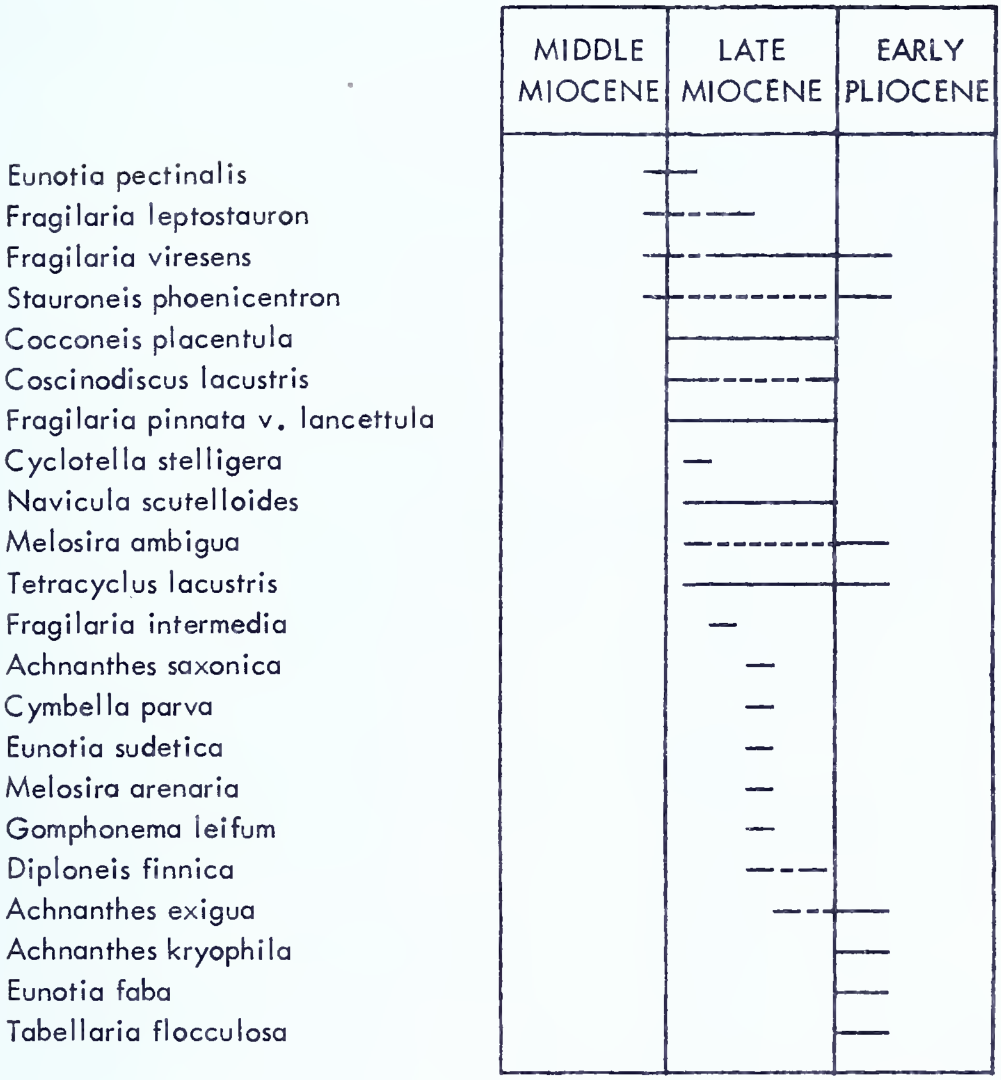


Figure 2. Occurrence of various diatoms from Middle Miocene to Early Pliocene.

no. 9

ABBREVIATIONS USED IN TABLES

Agardh	Aga.
Braun	Br.
de Brébisson	de Bré.
Cleve	Cl.
Ehrenberg	Ehr.
Gregory	Greg.
Grunow	Grun.
Hemprich	Hem.
Hêriband	Hêri.
Hustedt	Hust.
Krasske	Kr.
Kützing	Kü.
Moore	Mo.
Müller	Mü.
Östrup	Ös.
Petersen	Pe.
Rabenhorst	Rab.
Ralfs	Ra.
Roth	Roth.
Schumann	Schu.
Smith	Sm.
Van Heurck	Van He.
X	less than 0.5%.

no. 9

Table 1. Percentage of Diatoms from Aldrich Station.

	LATE MIOCENE					EARLY PLIOCENE
Lithologic Units fide Axelrod, 1956	A3	A4		A5		C1
	P1	P2	P5	P6	P8	P20
Achnanthes exigua Grun				2		2
A. hauckiana Grun					X	1
A. kryophila Pe						2
A. lanceolata (de Bré) Grun			1	12	2	1
A. lanceolata v. rostrata (Ös) Hust				2		
Cocconeis placentula Ehr		1	3	2	3	
Coscinodiscus lacustris Grun	3	13				
Cymbella turgida (Greg) Cl				1		
Eunotia faba (Ehr) Grun						X
E. pectinalis (Kü) Rab		1				
E. sudetica Mü			1			
Fragilaria brevistriata Grun		3	10	10	7	X
F. construens (Ehr) Grun	35	9	42	18	51	6
F. intermedia Grun			2			
F. leptostauron (Ehr) Hust			1			
F. pinnata Ehr	7		10	30	21	10
F. pinnata v. lancettula (Schu) Hust			1	2	1	
F. virescens Ra		1	10	10	4	1
Melosira ambigua (Grun) Mü		51				26
M. granulata (Ehr) Ra	39	315	833	520	899	
M. islandica Mü	16	11	6	8		8
M. italica (Ehr) Kü		8				14
M. italica v. valida Grun						19
Navicula scutelloides Sm				1		
Nitzschia amphibia Grun			6	1	11	X
Opephora martyi Heri						1
Stauroneis phoenicentron Ehr						X
Synedra vaucheriae Kü			5			X
Tabellaria flocculosa (Roth) Kü						5
Tetracyclus lacustris Ra		1	3	1	1	X

no. 9

Table 2. Percentage of Diatoms from Buffalo Canyon.

	MIDDLE MIOCENE					
	P1	P2	P3	P4	P5	P6
Achnanthes hauckiana Grun		1				
A. lanceolata (de Bre) Grun				1		
Coscinodiscus nevadensis n. sp.	96					
C. sp.			20		2	
Cymbella aspera (Ehr) Cl		X				
C. cistula (Hem) Grun		X		4	1	
C. turgida (Greg) Cl		44		3		
C. ventricosa Kü		2		11	3	
C. sp.		1		3	2	
Eunotia pectinalis (Kü) Rab						6
Fragilaria brevistriata Grun		X				
F. construens (Ehr) Grun	1	28	5	24		
F. pinnata Ehr		21	7	18	6	
F. virescens Ra						2
Gomphonema gracile Ehr						3
G. parvulum (Kü) Grun						27
G. sp.				X	1	3
Melosira distans (Ehr) Kü	150					
M. distans v. africana Mü	1					
M. granulata (Ehr) Ra	2		185	12	51	
M. islandica Mü	2100		68	8	33	1
M. italica (Ehr) Kü				7		47
Navicula anglica Ra v. subsalsa Grun						1
N. sp.						3
Nitzschia amphibia Grun				2		
Opephora martyi Héri		X				
Pinnularia major (Kü) Cl						2
P. microstauron (Ehr) Cl						1
P. nodosa (Ehr) Sm						X
P. sp.				X		2
Stauroneis phoenicentron Ehr						2
Synedra tabulata (Aga) Kü				X		
S. vaucheriae Kü		X		6	1	
S. sp.				1		
Tetracyclus rupestris (Br) Grun	1	1	X			

Table 3. Percentage of Diatoms from Ione Road.

	MIDDLE MIOCENE			
	P1	P2	P3	P4
Achnanthes lanceolata (de Bré) Grun v. elliptica Cl				1
A. sp.			5	
Cymbella aspera (Ehr) Cl		2		3
C. gastroides Kü		1		23
C. tumida (de Bré) Van He		3	5	1
C. ventricosa Kü		12	127	35
C. sp.		X	2	
Eunotia pectinalis (Kü) Rab			1	
Fragilaria brevistriata Grun		4	3	1
F. construens (Ehr) Grun		24	16	5
F. leptostauron (Ehr) Hust		1		
F. pinnata Ehr		15	11	5
F. viresens Ralfs				1
Gomphonema accuminatum Ehr		1		
Melosira distans v. africana Mü		28	55	11
Navicula cincta (Ehr) Kü		1		
N. sp.		2		
Nitzschia amphibia Grun		3		8
N. linearis Sm		1		
Synedra pulchella (Ralfs) Kü				1
S. tabulata (Aga) Kü			5	
S. vaucheriae Kü		2		3
Tetracyclus rupestris (Br) Grunov			1	2

no. 9

Table 4. Percentage of Diatoms from Stewart Valley.

	LATE MIOCENE								
	P1	P4	P5	P10	P11	P13	P15	P16	P17
Achnanthes lanceolata (de Bré) Grun		2	1	2	1	2	X	1	7
A. saxonica Kr					1				
A. sp.		1	X				X		
Coccaneis placentula Ehr		1	1	1			X	1	
Coscinodiscus lacustris Grun									4
Cyclotella stelligera Cl et Grun		1							
Cymbella parva (Sm) Cl					X				
C. turgida (Greg) Cl								X	
Diploneis finnica (Ehr) Cl				X			X		
Eunotia sp.	X	1						X	
Fragilaria brevistriata Grun							1	1	X
F. construens (Ehr) Grun	12	42	14	28	55	33	24	31	42
F. pinnata Ehr	9	14	5	9	16	5	3	8	18
F. pinnata v. lancettula (Schu) Hust	1	5		4	2	4	3	5	6
F. virescens Ra			X	X	1	1			
Gomphonema leifum n. sp.				1		1			
Melosira arenaria Mo	X			1					
M. granulata (Ehr) Ra	32	25	76	35	7	40	64	49	9
M. islandica Mü	36	8	3	2	15	12	4	3	13
M. italica (Ehr) Kü		1		17	1	1		X	1
Navicula scutelloides Sm		1	X	1	1	X		X	X
N. sp.	X								
Nitzschia amphibia Grun					X		X		
Tetracyclus lacustris Ra			X		X				4
T. rupestris (Braun) Grun					X		2	1	

no. 9

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PALEOBIOS

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 10 April 15, 1970

A RE-EVALUATION OF MANDIBLES OF ALLODESMUS (OTARIIDAE, CARNIVORA) FROM THE ROUND MOUNTAIN SILT, KERN COUNTY, CALIFORNIA

by

Lawrence G. Barnes

A RE-EVALUATION OF MANDIBLES OF ALLODESMUS (OTARIIDAE, CARNIVORA) FROM THE ROUND MOUNTAIN SILT, KERN COUNTY, CALIFORNIA

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ABSTRACT

A series of Allodesmus mandibles from the late middle Miocene Sharktooth Hill bonebed in the Round Mountain Silt of Kern County, California forms the basis for a study of the variation in a sample including the holotype of A. kelloggi Mitchell (1966). The range of variation in the sample encompasses the features of the holotype of A. kernensis Kellogg (1922), and A. kelloggi is therefore considered a junior synonym of A. kernensis. The mandibles show variation in the position of teeth and the development of other structures. The magnitude of variation is comparable to that in a series of mandibles of the living species Zalophus californianus Lesson.

INTRODUCTION

Kellogg (1922) described a new genus and species of otariid, Allodesmus kernensis, on the basis of an incomplete mandible from Miocene sediments east of Bakersfield, Kern County, California. In his monograph on mammals of the Sharktooth Hill bonebed in the Round Mountain Silt (Diepenbrock, 1933; Addicott, 1965; =Temblor Formation in the terminology of Kellogg, 1922, 1931; Mitchell, 1966), Kellogg (1931) assigned several additional mandibles, rostral fragments, and postcranial elements to A. kernensis. None of the mandibles was complete. Downs (1953) referred a nearly complete mandible from the Sharktooth Hill bonebed to A. kernensis. Extensive recent quarrying in the bonebed has led to the accumulation of a large number of bones of Allodesmus in collections of various institutions, and the genus is the most completely known fossil otariid. In 1960, Mitchell made an extensive quarry at Sharktooth Hill and collected a nearly complete skeleton from the bonebed. Mitchell (1966) referred the skeleton and other specimens previously reported from the Sharktooth Hill bonebed to a new species, A. kelloggi, and restricted A. kernensis Kellogg to the holotype, which Mitchell (1966, p. 34) believed to be distinct from the new species in mandibular features. He also concluded that the holotype of A. kernensis was collected stratigraphically lower than the bonebed.

The diagnosis and published photographs of A. kelloggi Mitchell are insufficient to adequately distinguish the species from the holotype of A. kernensis Kellogg. Diagnosis of the species A. kelloggi is : "Lower incisor 1 posterior and medial to incisor 2, diastem between lower premolar 4 and molar 1, ascending ramus of dentary with sharp lateral flange on external side,...". Unfortunately the description of the positions of the incisors also describes the arrangement in the holotype of A. kernensis. Other diagnostic features of the A. kelloggi holotype are subject to significant individual variation among other Allodesmus mandibles from the bonebed. To determine whether or not that variation encompasses the characteristics of the A. kernensis holotype, I have qualitatively and quantitatively analyzed the variation in a sample of mandibles from the bonebed, consisting of specimens collected by Mitchell and myself and those studied by Mitchell and Kellogg. A series of mandibles of Zalophus californianus californianus (Lesson) was studied to determine the amount of variation in a living species of otariid. I have also investigated the stratigraphic occurrence of the holotype of A. kernensis.

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Figures 2-5 and 9-10 were drawn by Mr. Owen Poe; figures 6-8 were drawn by Mrs. Patricia Lufkin, both Staff Artists of the Museum of Paleontology, University of California. Other illustrations are by the author.

METHODS

A long period of time may have elapsed during the accumulation of bones in the Sharktooth Hill bonebed, and the sample of mandibles studied here may represent individuals that died and were deposited over a period of hundreds or thousands of years. I assumed however that the sample is representative of a population and based discussions of general morphology and ontogenetic change on this premise.

All measurements were made with the same calipers and are given to the nearest millimeter. Kellogg's measurements of alveolar diameters of CAS 4395 are consistently smaller than those that I obtained, and may be attributable to matrix which remained in the alveoli until the present study. My measurements of the lengths of mandibular

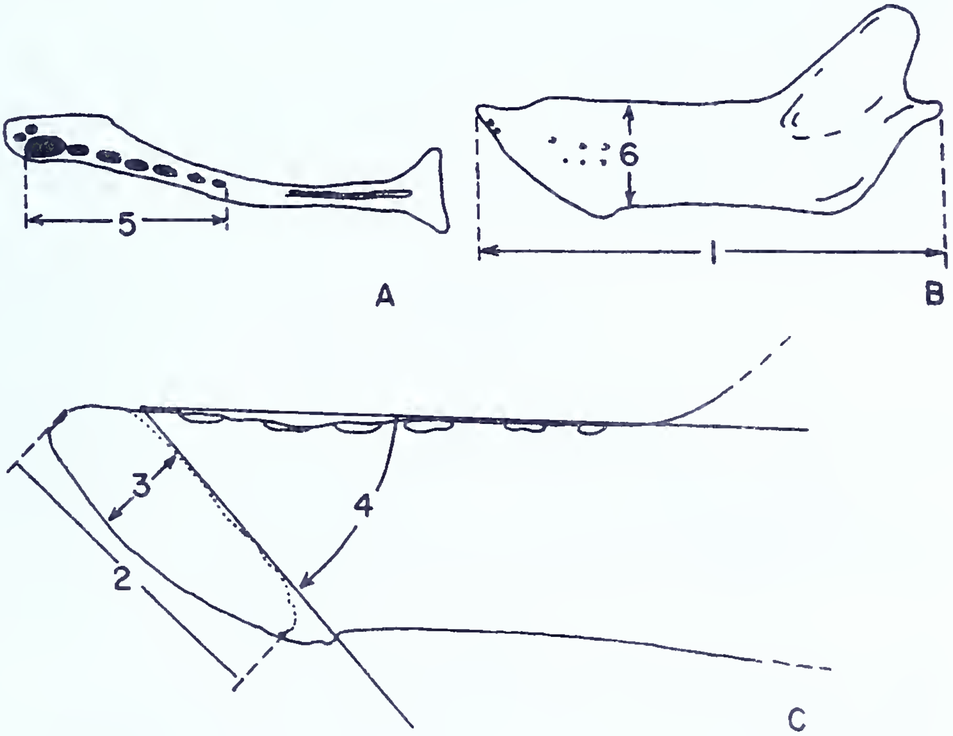

Fig. 1. Some dimensions of otariid mandibles used in this study: A, occlusal view; B, labial view of left mandible; C, lingual view of right mandible. 1, total length, mandibular condyle to chin; 2, greatest length of symphysis; 3, greatest breadth of symphysis; 4, angle between posterior border of symphysis and top of alveolar row; 5, length of alveolar row, C-M_2; 6, depth of horizontal ramus at P_3.

symphyses are generally smaller than those of Kellogg or Downs. I measured only the rugose portion of the symphysis and did not extend the measurement to include the ventral extremity of the genial tuberosity, which is sometimes variably developed and not involved in the suturing of the mandibles. The outline of the symphysis proper is distinct enough to afford measurements which may be duplicated within one millimeter. Measurements of the acute angle between the posterior border of the symphysis and the top of the alveolar row can be repeated with an accuracy of from one to two degrees (see fig. 1).

Text abbreviations are: CAS - California Academy of Sciences, LACM - Los Angeles County Museum of Natural History, LACM(CIT) - specimens originally in California Institute of Technology now housed in Los Angeles County Museum of Natural History, UCMP - University of California Museum of Paleontology, MVZ - University of California Museum of Vertebrate Zoology, and loc. - locality.

Abbreviations used in statistical tables are: N - number of observations, M - arithmetic mean, OR - observed range of values, S - standard deviation, X - the measurement in question, V - coefficient of variation, d - difference from mean. Statistical treatment follows Simpson and Roe (1939).

SYSTEMATICS

Genus ALLODESMUS Kellogg

Allodesmus kernensis Kellogg

Allodesmus kernensis Kellogg, 1922, Univ. Calif. Pub. Geol. Sci., vol. 13, p. 26.

Allodesmus kelloggi Mitchell, 1966, Univ. Calif. Pub. Geol. Sci., vol. 61, p. 4.

Type: CAS 2472, horizontal ramus of right mandible.

Type locality: CAS loc. 275. Kellogg (1922) described this locality as being 12 miles from Bakersfield and later as being near the center of Section 28, Township 28 South, Range 29 East (Caliente Sheet). The two descriptions do not coincide and other collecting data are contradictory (see Mitchell, 1966, p. 23). The description from the CAS locality catalog, "Kern River Miocene Coll., Chas. Morrice. 1 mile W. of Kern River, 4 miles above Oil City.", is little more definitive than Kellogg's description. In the center of Sec. 28, T. 28 S., R. 29 E., surface exposures are of Round Mountain Silt (Addicott, 1956, pls. 4, 10, and 11). Hanna stated (personal communication, 22 November 1968) that if Charles Morrice did collect the mandible, CAS 2472, it was probably found at Sharktooth Hill proper, Sec. 25, T. 28 S., R. 28 E. Therefore, if any of the locality data is correct, the type specimen was collected from the Round Mountain Silt.

Referred specimens:

CAS loc. 905

"In a fairly coarse, light gray, firm sandstone of Anderson's zone C, the uppermost fossil horizon of the Temblor Formation, on a hill west of Round Mountain, locally known as one of the Shark Tooth Hills. Near latitude 35° 28' North and longitude 119° 27' West, about 6.5 miles northeast of Bakersfield, 4 miles east of the Kern River Oil Field and 0.5 mile north of Kern River, Kern County, California. Section 25, Township 28 South, Range 28 East, Caliente Quadrangle, United States Geological Survey." (from CAS locality catalog).

Collected in 1924 by G D. Hanna and C. Morrice: CAS 4395, horizontal ramus of left mandible; CAS 4426, incomplete horizontal ramus of right mandible; CAS 4486, horizontal ramus of left mandible; CAS 4487, horizontal ramus of right mandible; CAS 4488, horizontal ramus of left mandible; CAS 4489, anterior end of right mandible; CAS 4490, anterior end of left mandible.

CIT loc. 49B

"....about 9 miles N. E. of Bakersfield, S. E. 1/4 sec. of sec. 23, T 28 S, R 28 E, Mt. Diablo base meridian....approximately 1 1/4 miles N. W. of Sharktooth Hill...." (Downs, 1953).

Collected in 1927 by California Institute of Technology personnel: LACM(CIT) 1204, right mandible lacking coronoid process.

LACM loc. 1557 = UCMP loc. V-6323

"....730 feet east and 1,193 feet north of the southwest corner of section 25, T. 28 S., R. 28 E., Oil Center Quadrangle (USGS, 1954), Kern County, California." (Mitchell, 1966). Approximate latitude and longitude are 35° 27' 30" N, 118° 55' 7.5" W. Elevation is about 680 feet, in the Sharktooth Hill bonebed, Round Mountain Silt.

Collected 1 October 1960 by E. D. Mitchell, J. Arndt, J. H. Lipps, and A. Warne: LACM 4320, complete right and left mandibles, belonging to a skeleton, holotype of *A. kelloggi* Mitchell, 1966.

TABLE 1. Measurements of *Allodesmus* mandibles (in cm unless indicated otherwise, parentheses indicate estimated measurements).

	CAS 2472*	CAS 4395	CAS 4426	CAS 4486	LACM 21092
Total length, glenoid to chin	----	----	----	----	----
Length alveolar row, C-M_2	14.1	14.3	----	----	11.2***
Length of symphysis	(9.5)	10.4	----	----	7.8
Breadth of symphysis	4.2	3.5	----	----	2.9
Depth of ramus at P_3	7.3	6.6	----	----	5.2
Depth of ramus at P_4	----	6.3	6.2	(5.7)	5.1
Angle, symphysis-alveolar row	45°	40°	----	----	46°
Anteroposterior dia. alveolus I_1	0.9	(1.2)	----	----	0.7
" " " I_2	1.4	(1.1)	----	----	1.0
" " " C	3.1	3.3	----	----	2.2
" " " P_1	1.6	1.6	----	----	1.4
" " " P_2	1.7	1.7	----	----	1.4
" " " P_3	1.7	1.7	(1.8)	1.6	1.6
" " " P_4	1.9	1.9	(1.7)	1.7	1.7
" " " M_1	1.9	1.5	1.4	1.4	1.7
" " " M_2	1.1	1.1	(0.9)	1.0	***
Length C-P_1 septum	0.7	0.7	----	----	0.4
" P_1-P_2 "	0.1	0.1	----	----	0.2
" P_2-P_3 "	0.1	0.1	----	0.3	0.1
" P_3-P_4 "	0.1	0.2	0.4	0.5	0.1
" P_4-M_1 "	0.1	0.6	0.5	0.6	0.4
" M_1-M_2 "	0.1	0.2	0.3	0.1	***

* Holotype of *Allodesmus kernensis* Kellogg, 1922.

** Holotype of *Allodesmus kelloggi* Mitchell, 1966.

*** C-M_1, M_2 not present.

LACM	LACM (CIT)	UCMP	LACM 4320**		UCMP	UCMP	UCMP	CAS	CAS	CAS	CAS
21753	1204	81708	left	right	81706	81707	81704	4489	4487	4488	4490
----	32.2	31.0	27.2	27.6	----	----	----	----	----	----	----
12.8	14.5	14.6	13.2	13.2	----	----	12.7	----	(11.0)	(10.5)	----
8.2	11.5	8.7	7.7	7.7	----	7.8	8.1	(7.5)	7.3	(6.8)	----
2.8		3.0	2.7	2.7	----	3.4	(2.7)	2.5	2.9	2.6	(2.3)
5.5	6.6	5.9	5.1	5.2	5.9	5.4	5.2	----	4.6	(4.2)	(5.0)
5.2	6.7	5.9	5.2	5.2	5.7	----	5.0	----	4.6	4.4	----
43°	39°	43°	(45°)	(45°)	----	45°	35°	(40°)	39°	36°	----
0.7	0.5	1.1	(0.9)	(0.8)	----	(1.0)	0.9	0.9	0.9	(0.6)	----
1.2	0.7	1.5	1.2	(0.9)	----	1.1	----	1.0	1.2	----	----
2.9	2.8	3.0	2.6	2.7	----	2.9	(2.5)	2.2	2.7	(2.5)	----
1.4	1.5	1.5	1.1	1.2	1.5	1.4	1.4	1.5	1.2	1.0	----
1.6	1.6	1.6	1.2	1.3	1.6	1.6	1.6	1.6	1.3	1.3	(1.4)
1.7	1.5	1.6	1.3	1.3	1.6	----	1.5	----	1.4	1.4	(1.4)
1.8	1.5	1.8	1.3	1.3	----	----	1.8	----	1.4	1.3	----
1.7	1.2	1.4	1.0	1.1	----	----	1.4	----	(0.9)	(0.8)	----
0.8	0.5	1.2	0.8	0.8	----	----	(0.9)	----	(0.4)	----	----
0.1		0.7	0.8	0.9	(0.6)	0.2	0.6	0.5	0.4	0.3	----
0.1		0.2	0.3	0.3	0.2	0.1	0.3	0.1	0.1	0.2	0.2
0.1		0.3	0.2	0.3	0.2	0.4	0.3	0.1	0.2	0.2	(0.2)
0.1		0.5	0.6	0.4	0.3	----	0.4	----	0.5	0.5	(0.4)
0.2		0.8	1.2	1.1	----	----	0.3	----	0.6	0.6	----
0.1		0.1	0.8	0.7	----	----	0.1	----	(0.2)	----	----

TABLE 2. Tabulation of structures in *Allodesmus* mandibles.

Specimen number	P_4–M_1 "diastem"	M_1 root	M_2 alveolus	Cheek tooth root constriction	Development of genial tuberosity	Mandibular thickness	Coronoid process	Inferred relative age	Sex
CAS 2472	small	bilobed	large	advanced	-----	thick	-----	adult	male?
CAS 4395	moderate	cylindrical	medium	slight	strong	thick	-----	adult	male?
CAS 4426	moderate	bilobed	medium, deep	advanced	strong	medium	-----	adult	male?
CAS 4486	moderate	bilobed	medium	advanced	-----	medium	-----	adult	male?
CAS 4487	moderate	cylindrical	-----	slight	moderate	thin	-----	subadult, immature	?
CAS 4488	moderate	cylindrical	-----	absent	slight	thin	-----	immature	?
CAS 4489	-----	-----	-----	advanced	-----	medium	-----	mature	female?
CAS 4490	-----	-----	-----	moderate	moderate	thin	-----	subadult	?
LACM 4320	large	cylindrical	small	slight	strong	thick	expanded	adult	male
LACM 21753	small	bilobed	medium	moderate	slight	thin	-----	subadult	male?
LACM 21092	small	bilobed	absent	slight	moderate	thin	-----	subadult	female?
LACM(CIT)1204	moderate	double	small	advanced	strong	thin	thin	adult	male?
UCMP 81704	small	bilobed	small	slight	moderate?	medium	-----	subadult	male?
UCMP 81706	-----	-----	-----	slight	moderate	thick	-----	subadult	male?
UCMP 81707	-----	-----	-----	slight	slight	medium	-----	subadult	male?
UCMP 81708	moderate	double	small	moderate	strong	thin	thin	subadult	male?

Collected March 1965 by L. G. Barnes: UCMP 81704, horizontal ramus of left mandible; UCMP 81705, fragment of angle of right mandible.

LACM loc. 1625 = UCMP loc. V-6324

Kern County, California; SW 1/4, SW 1/4 Sec. 25, T 28 S, R 28 E, at an elevation of about 670 feet on the east face of a southward trending ridge, a few feet east of power lines, 300 feet south of LACM loc. 1557 = UCMP loc. V-6323, 35° 27' 30" N., 118° 55' 7.5" W., Oil Center 7.5 minute topographic map, USGS, 1954. Collected from Sharktooth Hill bonebed, Round Mountain Silt.

Collected 20 August 1963 by E. D. Mitchell and C. Swift: LACM 21092, horizontal ramus of left mandible, incomplete horizontal ramus of right mandible.

Collected 18 August 1963 by C. Swift and E. D. Mitchell: LACM 21753, horizontal ramus of right mandible.

UCMP loc. V-6843

Kern County, California; SW 1/4, SW 1/4 Sec. 25, T 28 S, R 28 E, at an elevation of about 700 feet near the south end of the west face of a north-south trending ridge, 400 feet due east of LACM loc. 1557 = UCMP loc. V-6323, 35° 27' 33.5" N., 118° 55' 2.5" W., Oil Center 7.5 minute topographic map, USGS, 1954. In Sharktooth Hill bonebed, Round Mountain Silt.

Collected 24 March 1967 by W. H. Barnes, S. E. Barnes, L. G. Barnes: UCMP 81708, complete right mandible, associated with skull.

UCMP loc. V-68131

Kern County, California; SW 1/4, SW 1/4 Sec. 25, T 28 S, R 28 E, at an elevation of about 700 feet on west face of a southward trending ridge, about one-third the distance south from head of the canyon toward south end of ridge, 375 feet northeast of LACM loc. 1557 = UCMP loc. V-6323, 35° 27' 35" N., 118° 55' 4" W., Oil Center 7.5 minute topographic map, USGS, 1954. In Sharktooth Hill bonebed, Round Mountain Silt.

Collected 18 April 1966 by L. G. Barnes: UCMP 81707, anterior end of left mandible.

Collected 24 April 1966 by L. G. Barnes: UCMP 81706, horizontal ramus of left mandible.

DESCRIPTION OF THE MANDIBLE OF ALLODESMUS

This description is purposely structured to apply to any Allodesmus mandible now known from the Sharktooth Hill bonebed. A detailed

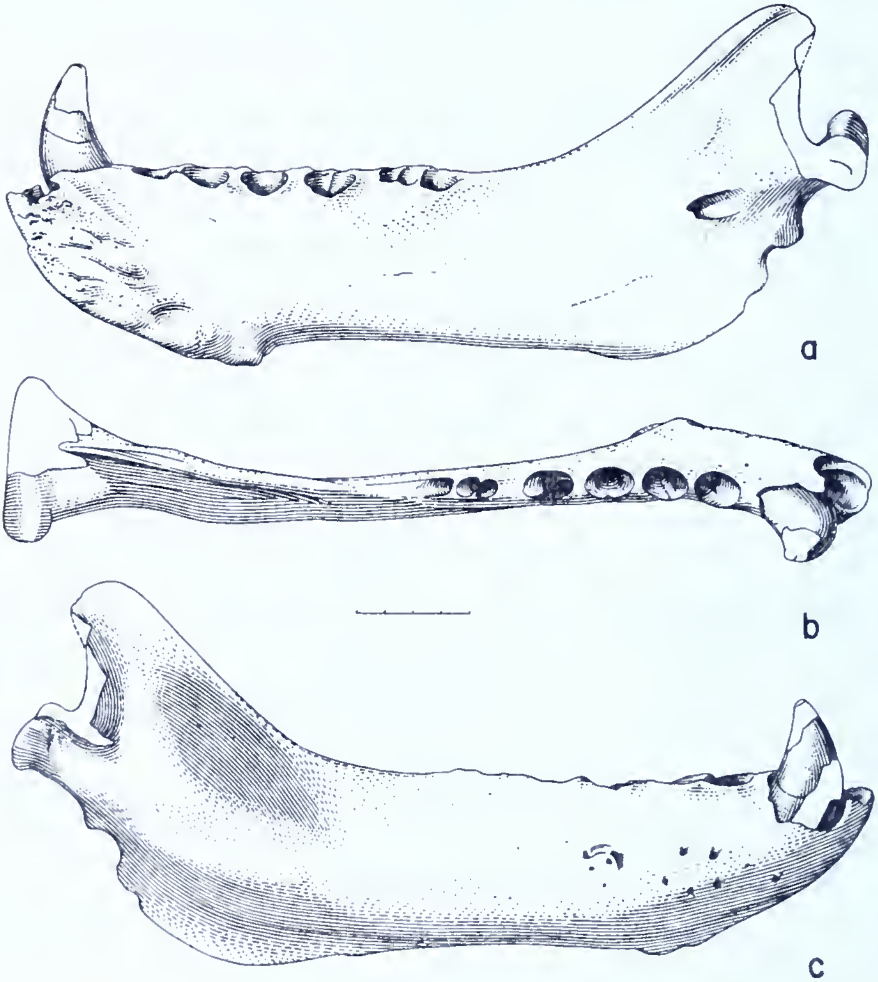

Fig. 2. *Allodesmus kernensis* Kellogg, right mandible with canine, UCMP 81708, loc. V-6843: a, lingual view; b, acclusal view; c, labial view; scale line equals 4 cm.

description of LACM 4320 may be faund in Mitchell (1966) and need not be duplicated here. *Allodesmus* has an elongate and deep mandible with the alveolar row accupying at least one-half of its length. A large and posteriorly directed coronoid process rises gently from a point slightly posterior to the last cheek taoth. The anterior border of the symphysis curves anteriorly and dorsally from a usually praminent genial tuberosity. Dorsal and ventral margins of the horizontal ramus are nearly parallel, but the ventral margin is slightly concave dorsally. Only a small angular process interrupts the smooth curve of the convex angle of the mandible. At a point slightly dorsal to the level of the alveolar row is the mandibular condyle, directed strongly posteriorly. The masseteric fossa is large and shallow. The horizontal ramus is flat, massive anteriorly, and thin ventral to the ascending ramus.

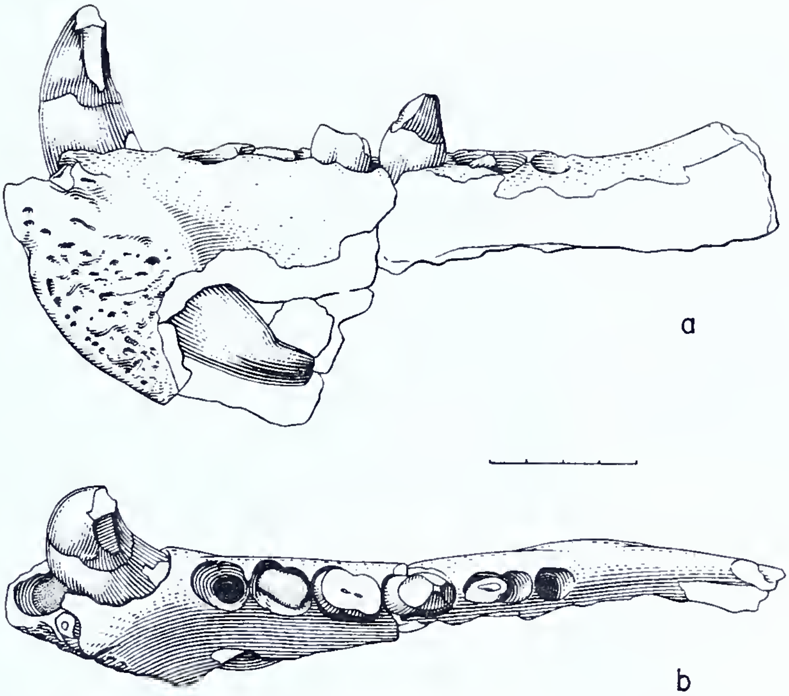

Fig. 3. *Allodesmus kernensis* Kellogg, holotype, horizontal ramus of right mandible with C, P_4, and roots of medial I and P_3, CAS 2472, loc. 275: a, lingual view; b, occlusal view; scale line equals 4 cm.

A sulcus on the right mandible of LACM 4320, just posterior to the genial tuberosity, was described by Mitchell (1966, p. 6) as a possible tract for a branch of the external maxillary artery. No other mandible in the sample has such a sulcus, and I consider it to be a pathologic feature. The bone surface around the sulcus on LACM 4320 is almost identical to that around bone lesions on mandibles of Recent Otariidae.

Normally, the mandible contains two incisors, one canine, four premolars, and two molars. The medial incisor is situated diagonally posteromedial to the larger lateral incisor. The canine is long, has a conical crown which is curved posteriorly at the apex, and bears a root which is oval in cross section and extends the full length of the symphysis. It causes the anterior corner of the horizontal ramus to protrude laterally beyond the otherwise nearly flat external surface. The cheek tooth series of premolars and molars forms a straight line. P_1 is single rooted and has a cylindrical alveolus. Roots of subsequent four teeth (P_2 through M_1) are vertically constricted, more strongly on labial side than on lingual side, so that they are bilobed, sometimes bifurcated at their tips, or distinctly two rooted. The amount of separation of the two lobes of single roots is progressively greater posteriorly to M_1, which is sometimes

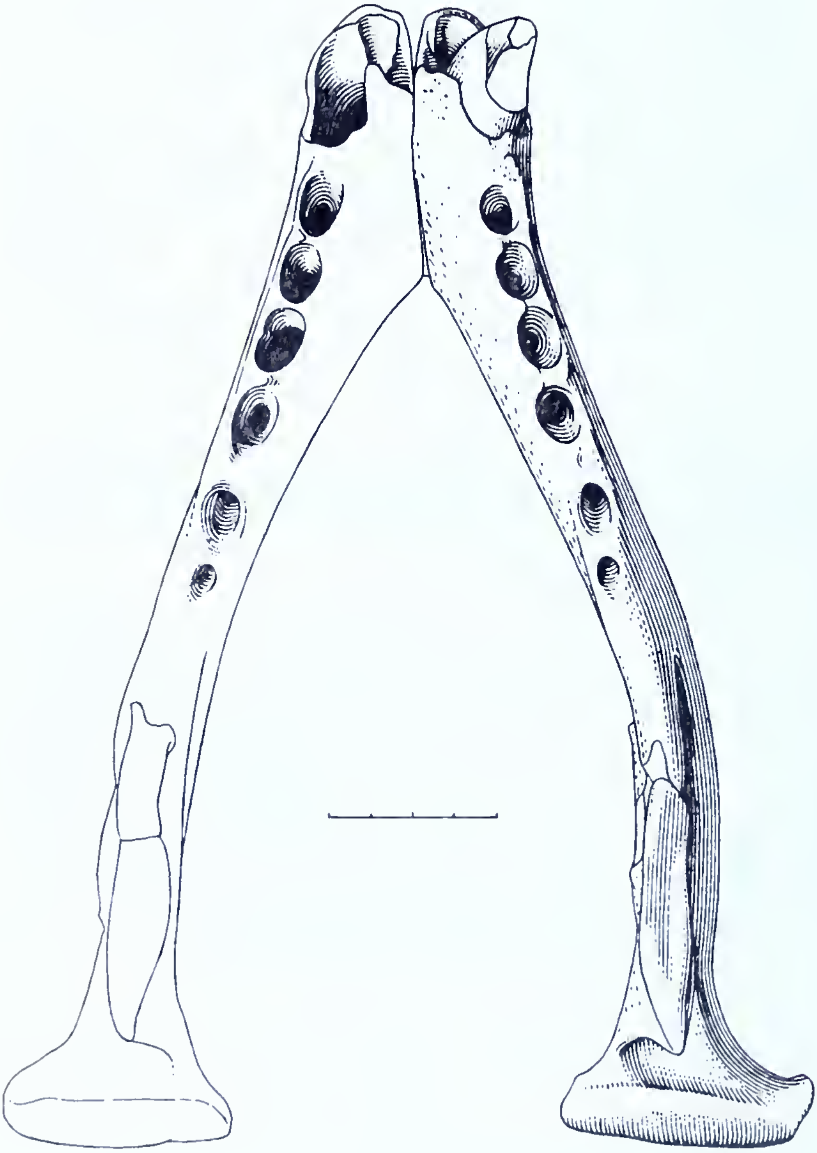

Fig. 4. Allodesmus kernensis Kellogg, (holotype of Allodesmus kelloggi Mitchell), right and left mandibles with right C, LACM 4320, loc. 1557: occlusal view; scale line equals 4 cm.

two rooted. Only one-third of the mandibles have M_1 with a cylindrical root. M_2 consistently has a single, cylindrical root. The bilobed and double rooted condition of P_2 through M_1 may be regarded as a relic of a primitive two rooted condition.

Sometimes one or three, but usually two, nutrient foramina occur below the incisors, and six to eleven nutrient foramina appear on the external surface of the horizontal ramus below the canine and anterior cheek teeth.

ONTOGENETIC CHANGES IN ALLODESMUS MANDIBLES

Larger mandibles assigned to Allodesmus may belong to mature males and smaller ones to mature females or immature males. Kellogg (1931, p. 227-231) used size differences to subdivide the sample of specimens he studied. Basis for such a separation lies in the assumption that Allodesmus displayed sexual dimorphism as do living Otariidae. Among Recent species, mature males are larger and have more robust bones than do mature females, and bones become more rugose with increased age of the individual. In size, bones of mature females are comparable to those of immature males, but other osteological characters linked with ontogeny indicate sexual distinction.

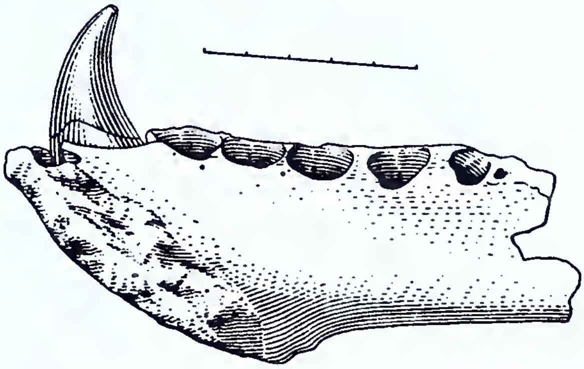

Fig. 5. Allodesmus kernensis Kellogg, horizontal ramus of right mandible, with canine, CAS 4487, loc. 905: lingual view; scale line equals 5 cm.

Upon eruption, cheek teeth of living species of Otariidae have only a short, cylindrical, and hollow stem of the root present. During later ontogeny roots of post-P_1 cheek teeth develop into either bilobed, bifurcated, or two-rooted structures depending upon the taxon and position in the mouth. This age-linked feature of root formation coincides with progressive development of transverse septa in alveoli containing teeth with bifurcated and double roots, or of vertical ridges of bone on the internal surface of the labial wall and sometimes the lingual wall of alveoli containing bilobed single rooted teeth.

In alveoli of cheek teeth of Allodesmus, similar transverse septa and vertical ridges are present (see fig. 6), which, though few teeth are ever preserved in place, may be used as an indicator of root development. Larger mandibles of Allodesmus possess all stages of root constriction: 1) UCMP 81704 - P_4 and M_1 slightly constricted; 2) UCMP 81708 (fig. 2) - a medium sized mandible with P_4 strongly constricted, M_1 with a complete alveolar septum, and P_{2-3} and M_2 constricted; 3) LACM (CIT) 1204 - P_{2-4} and M_1 constricted; 4) CAS 4426 and 4486 - extremely large mandibles and have P_{3-4} and M_1 constricted. The small mandible, CAS 4489, has advanced root constriction and may be an adult female. A mandible of comparable size, CAS 4488, has no root constriction and may be from an immature individual.

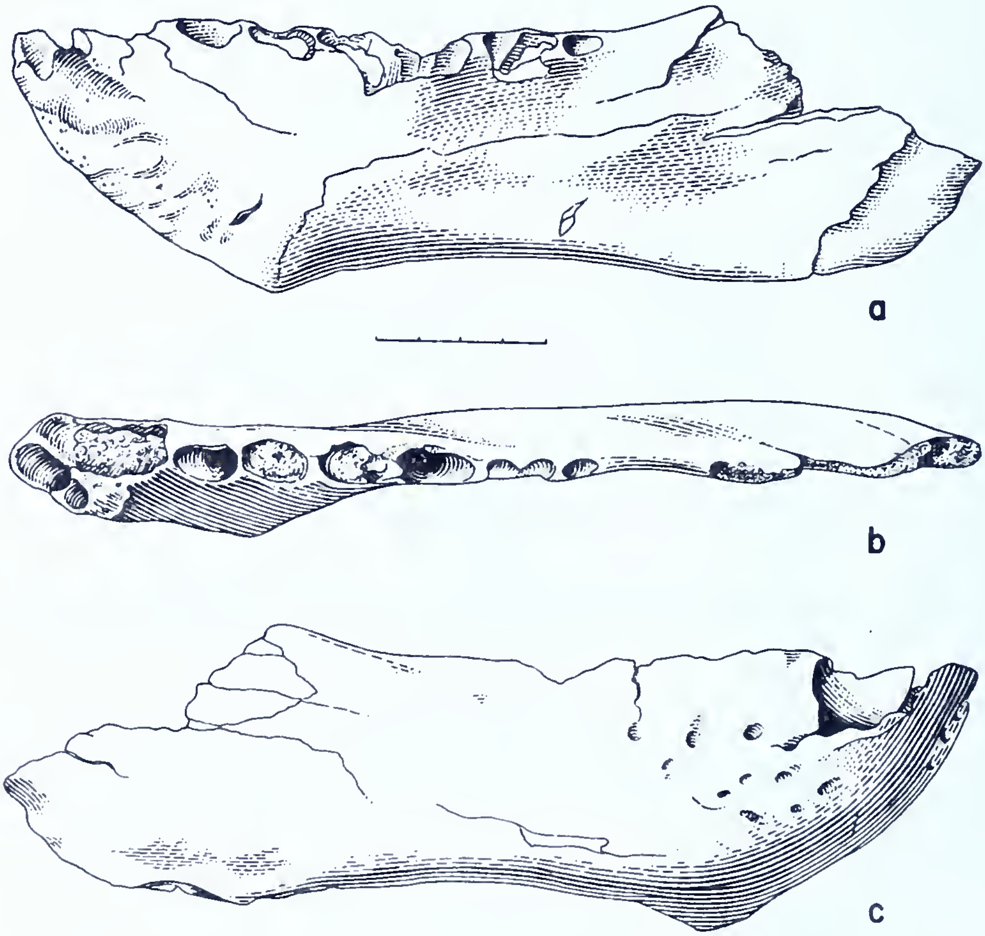

Fig. 6. Allodesmus kernensis Kellogg, horizontal ramus of right mandible, LACM 21753, loc. 1625: a, lingual view; b, occlusal view; c, labial view; scale line equals 4 cm.

Other changes in the mandible linked with increased maturity are: lengthening and broadening of mandibular symphysis, lengthening of alveolar row, deepening of horizontal ramus, and increase in alveolar diameter. Each of these dimensions, while increasing with size of individuals, does not show a proportionate increase from one individual to a larger one in the series.

A definitive index of age among the Otariidae is the increase in diameter and in length of the tooth roots as they emerge from the alveoli by the addition of annulae of dentine (Scheffer, 1950; Chiasson, 1957). The same condition was shown to exist in *Allodesmus* by Mitchell (1966, p. 20-21) who concluded that the age of some specimens was at least thirteen years. Alveoli generally reflect the increased diameter of the roots, however their increase is not proportionate to the overall size increase of the mandible. Smaller mandibles have proportionately larger alveolar diameters, as in immature *Zalophus californianus*.

INDIVIDUAL VARIATION

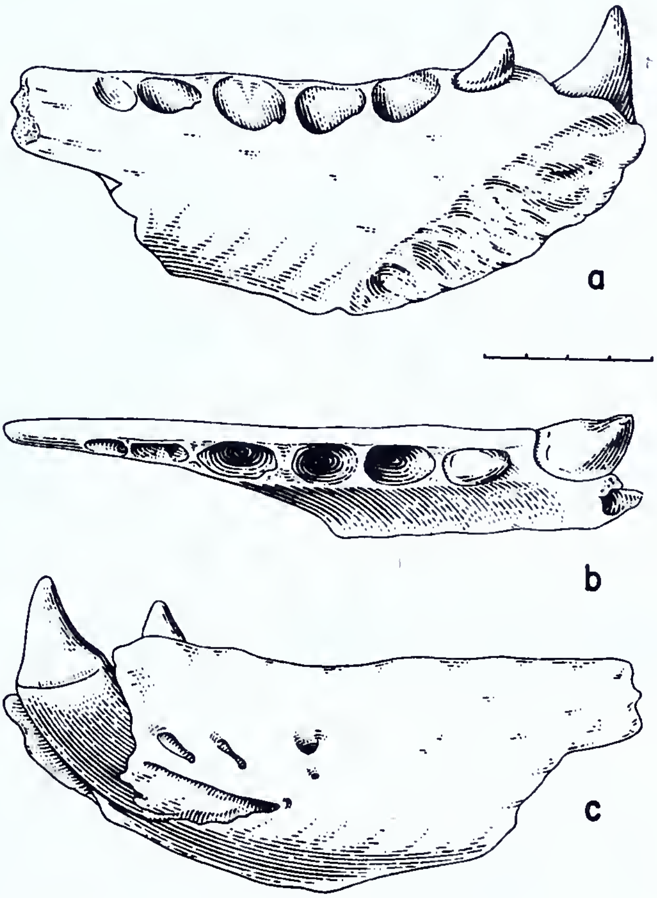

Fig. 7. *Allodesmus kernensis* Kellogg, horizontal ramus of left mandible with C and P_1, UCMP 81704, loc. V-6323: *a*, lingual view; b, occlusal view; c, labial view; scale line equals 4 cm.

Alveoli of the incisors are variable in their positions and in the degree of formation of a complete alveolar rim. In UCMP 81707, LACM 4320, 21092, and 21753, the medial incisor is closely appressed to the canine alveolus, while in most other bonebed mandibles the alveolus for the medial incisor is at least 3 mm from the alveolus for the canine.

The symphysis of bonebed mandibles is generally elongate, narrow at the base, wider at the apex, but widest about one-third the distance from the apex. UCMP 81704 (fig. 7) has an unusually long symphysis for its width, whereas the widest point of the symphysis of UCMP 81707 (fig. 8) is located more centrally therefore giving it a more rounded shape. The angle between the posterior margin of the symphysis and the top of the alveolar row ranges between 35° and 46°, and is independent of the size of the mandible.

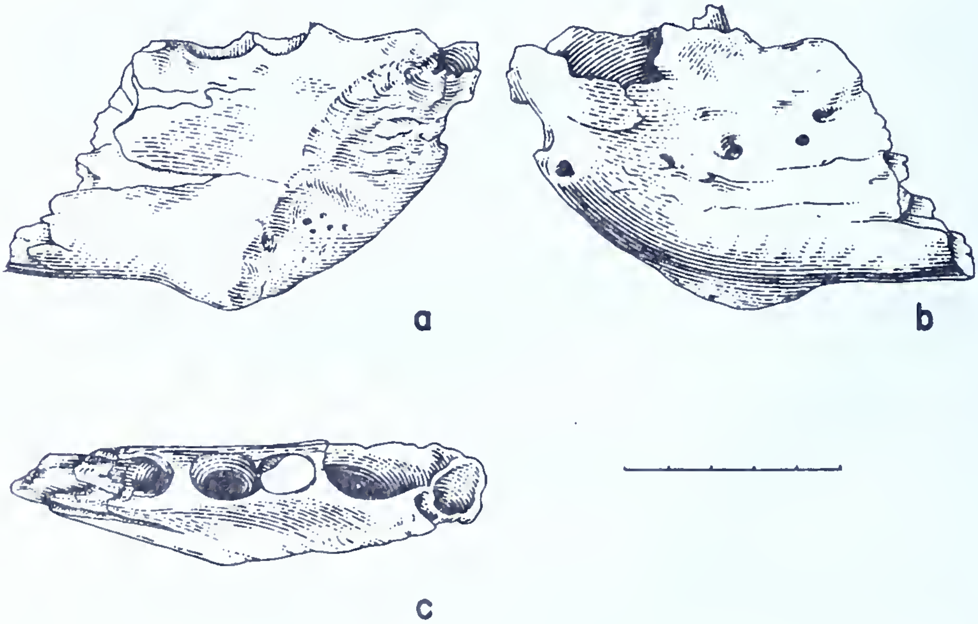

Fig. 8. Allodesmus kernensis Kellogg, anterior end of left mandible with root of P_1, UCMP 81707, loc. V-68131: a, lingual view; b, labial view; c, occlusal view; scale line equals 5 cm.

Septal thicknesses between cheek teeth vary randomly and are not related to size or maturity of the specimen. As Mitchell's (1966) plate 4 and fig. 4, this paper, indicate, the interalveolar septa between cheek teeth thicken progressively posteriorly in the mandible of LACM 4320. Such progressive increase in septal thickness exists in some bonebed mandibles, although some (CAS 4395, LACM 21753) have more closely spaced teeth. The P_4-M_1 diastem is variably developed: largest in LACM 4320, less so in UCMP 81708 (fig. 2), and smaller than or comparable to that between any of the other cheek teeth in UCMP 81704 (fig. 7), LACM 21753 (fig. 6), and LACM 21092 (fig. 9).

In addition to variable positioning of cheek teeth, a notable amount of variation occurs in the reduction or complete absence of teeth. Molars are reduced; their alveoli are usually half the depth of those of premolars. Molar alveoli of LACM 4320 and UCMP 81708 are shallow, but M_2 of CAS 4426 has an unusually deep alveolus. LACM 21092 has no alveoli for M_2 on either side (fig. 9), yet there is space posterior to M_1 for such a tooth. The variation encountered in lower molars of the mandibles suggests that in the population of Allodesmus the lower molars may have been in the process of being lost altogether. Loss of molars and retention of premolars is a specialization of the walruses. In LACM 4320, CAS 4487, and CAS 4488, M_1 has one cylindrical root, but in LACM 21092, CAS 4486, CAS 4426, LACM 21753, UCMP 81704, and CAS 4395 M_1 has an anteroposteriorly bilobed root, and in UCMP 81708, M_1 had two roots.

The thickness of the horizontal ramus has no directly proportional relationship to overall size in the sample. CAS 4486, LACM 21753, LACM(CIT) 1204, UCMP 81704, and UCMP 81708 are mandibles of fairly large size, yet they are thin and finely sculptured. In contrast, LACM 4320, CAS 4395, UCMP 81706, and UCMP 81707 are more robust mandibles. They are thicker transversely, and alveolar walls for cheek teeth are thicker.

The masseteric fossa in LACM 4320 is well delineated and highly sculptured, in LACM(CIT) 1204 the fossa is well delineated but smooth, and in UCMP 81708, the fossa is poorly delineated and smooth. In LACM 4320 (fig. 4), the anterior surface of the coronoid process is expanded and flattened, the condition referred to by Mitchell as a sharp lateral flange. I have not observed this condition on any other mandible of Allodesmus, however it does develop on the mandibles of some terrestrial carnivores and may be an age feature in Allodesmus.

The angle of the mandible is smooth and flat in UCMP 81708 and LACM 21753, while in LACM 4320 and UCMP 81705 it is rugose with a slight deflection of the external border.

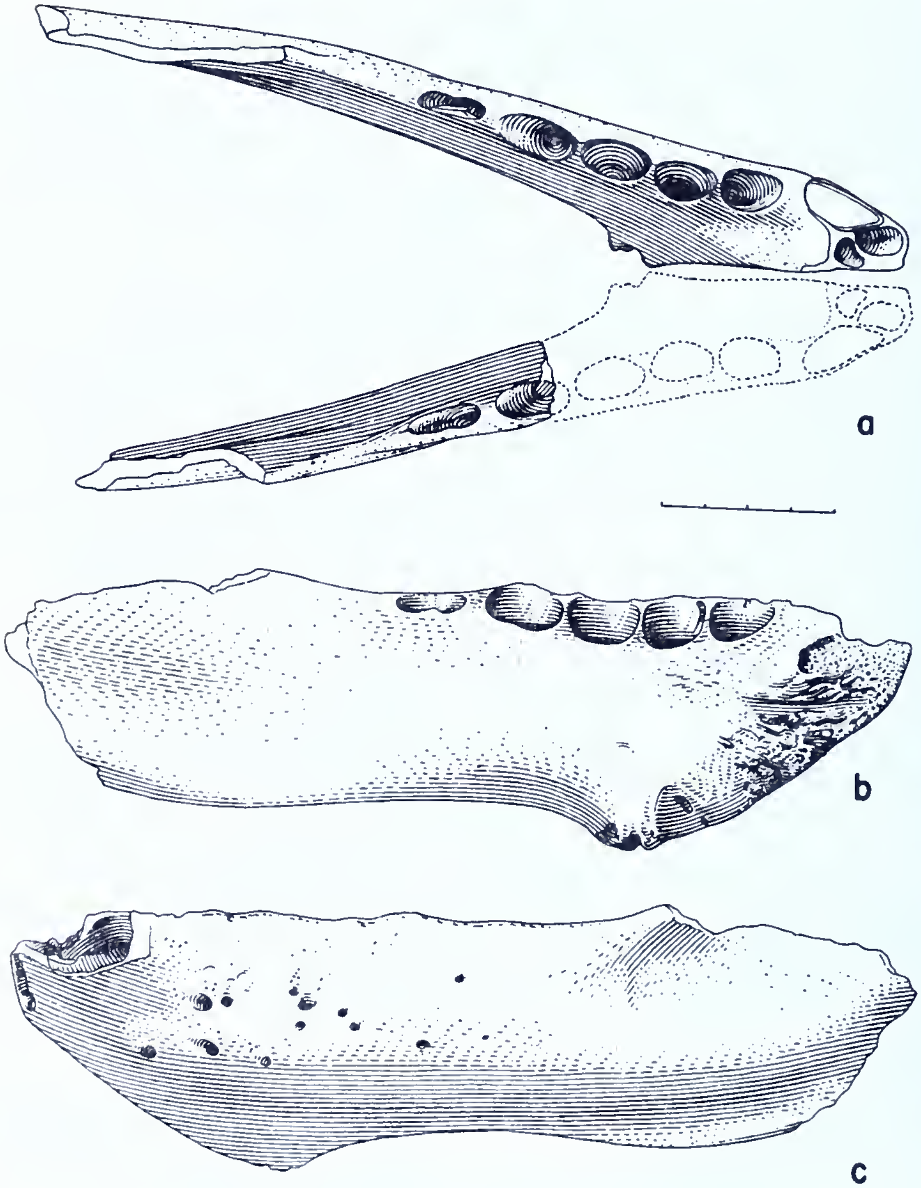

Fig. 9. *Allodesmus kernensis* Kellogg, LACM 21092, loc. 1625: a, incomplete horizontal ramus of right mandible, horizontal ramus of left mandible, dashed outline restored from left side, occlusal view; b, lingual view of horizontal ramus of left mandible; c, labial view of horizontal ramus of left mandible; scale line equals 4 cm.

The genial tuberosity is variably developed. In bonebed mandibles, this structure usually forms a prominence ventral and posterior to, and distinct from the ventral extent of the symphyseal surface. In UCMP

81707 (fig. 8) however, the genial tuberosity is much reduced, and the ventral margin of the symphysis forms the main prominence in this area.

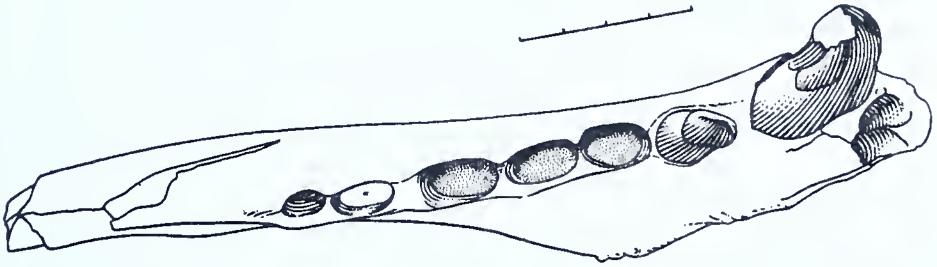

Fig. 10. *Allodesmus kernensis* Kellogg, horizontal ramus of left mandible with C and P_1, CAS 4395, loc. 905: occlusal view; scale line equals 4 cm.

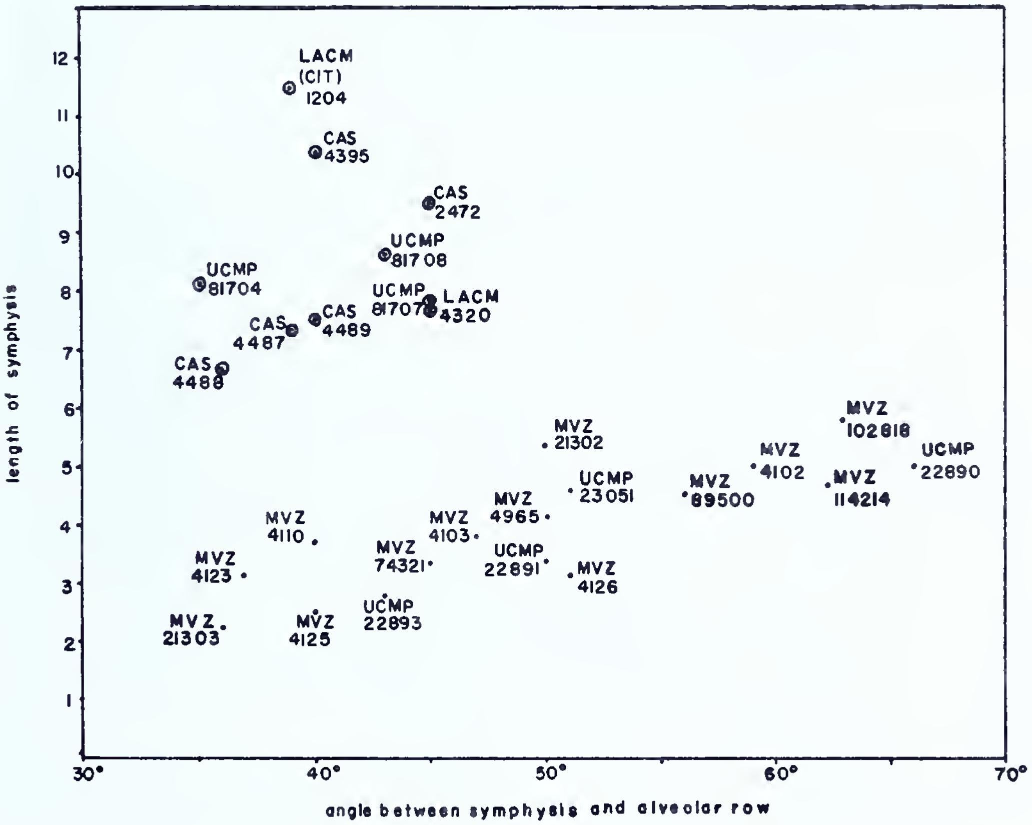

Fig. 11. Scatter diagram relating the greatest length of the symphysis (in cm) to the angle between the posterior border of the symphysis and the top of the alveolar row in mandibles of *Allodesmus kernensis* (represented by circled dots) and *Zalophus californianus* (represented by dots). CAS 2472 (holotype of *A. kernensis* Kellogg), LACM 4320 (holotype of *A. kelloggi* Mitchell).

The number of mental foramina on the anterior labial face of the horizontal ramus varies from six to eleven and their positions are highly variable. One to three foramina may be located on the anterior surface of the mandible below the incisors.

COMPARISON WITH VARIATION IN *ZALOPHUS CALIFORNIANUS*

In analyzing variation in mandibles of *Allodesmus* from the Sharktooth Hill bonebed, a series of skulls and mandibles of male and female adult specimens of *Zalophus californianus californianus* (Lesson) were used for comparison and control. Measurements and statistical computations of the same type as those made for *Allodesmus* were obtained, using the right mandible of each individual. Both sexes were used because the *Allodesmus* sample is not segregated.

Material Studied

Females: MVZ 4101, 4103, 4110, 21303, and 4126, UCMP 22891. Males: MVZ 4102, 4111, 4123, 4125, 4965, 21302, 74321, 89500, 102818, 112387, and 114214, UCMP 23051, 22888, and 22890.

Interpretation

In the sample of *Zalophus* mandibles, measurements of the alveolar row length, symphyseal length and breadth, and depth of the horizontal ramus do not increase in proportion with the overall increase in mandibular length. Such was seen in *Allodesmus* also. The general conformation of the *Z. c. californianus* mandible, particularly the symphyseal shape, is much more constant than in *Allodesmus*, although the dentition is more variable. In nearly half of the *Zalophus* skulls studied M^2 was present on one or both sides. Supernumerary incisors are seen on some specimens, while some others lack cheek teeth or incisors. One adult male (MVZ 21302) had an unusually flattened chin, and one female (MVZ 4126) had greater than average interalveolar distances.

The space between the lower canine and P_1 is highly variable in *Zalophus* and is not always linked with age. All young animals have a short septum, but during ontogeny this separation may increase six-fold in some individuals or not at all in others. Generally, the remainder of the cheek teeth have rather uniform interalveolar septa with the P_3-P_4 septum usually 1 mm larger than the rest.

TABLE 3. Statistical data on *Allodesmus* mandibles from the Sharktooth Hill bonebed (in cm unless indicated otherwise).

	N	OR	M	S	V
Length alveolar row, C-M_2	8	10.5-14.6	13.0	1.45	11.1
Length of symphysis	12	6.8-11.5	8.2	1.34	16.3
Breadth of symphysis	11	2.3-3.5	2.8	0.34	12.1
Angle, symphysis-alveolar row	11	35°-46°	41°	3.5°	8.5
Anteroposterior dia. alv. M_1	11	0.8-1.7	1.3	0.28	21.5
Length P_4-M_1 septum	10	0.3-1.2	0.6	0.25	41.7

TABLE 4. Statistical data on right mandibles of *Zalophus californianus californianus* (in cm unless indicated otherwise).

	N	OR	M	S	V
Length alveolar row, C-M_1	18	5.6-8.6	7.1	0.90	12.7
Length of symphysis	18	3.1-5.8	4.4	0.74	16.8
Breadth of symphysis	18	1.4-3.3	2.4	0.57	23.8
Angle, symphysis-alveolar row	17	40°-66°	52°	6.9°	13.3
Anteroposterior dia. alv. M_1	18	0.8-1.3	1.0	0.13	13.0
Length P_4-M_1 septum	18	0-0.3	0.13	0.068	52.4

Permanent incisors of youngest specimens studied were fully erupted, and their alveoli do not increase in diameter with age. This was apparently true in *Allodesmus*.

Lengthening of the symphysis and deepening of the horizontal ramus with age was proportionate in both *Zalophus* and *Allodesmus*. The variable condition of the lower molars in *Allodesmus* is paralleled by that of the upper molars in *Zalophus*. Coefficients of variation (Tables 3 and 4) are high for both samples and higher for *Zalophus* than for *Allodesmus* in five out of six mandibular dimensions and reflect the extreme individual and sexual variation in these otariids.

CONCLUSIONS

Mitchell (1966, p. 34) in his comparisons between the holotype of *Allodesmus kernensis* (CAS 2472) and the mandible of the holotype of *Allodesmus kelloggi* (LACM 4320) included several of the features of the mandible which could be of diagnostic importance. In establishing the diagnosis of the new species, he relied upon differences between the two holotypes. Each of Mitchell's distinctions between the restricted *A. kernensis* (CAS 2472) and the holotype of *A. kelloggi* is discussed below in the light of the variation in the Sharktooth Hill bonebed sample revealed in the present study.

TABLE 5. Statistical comparison of *Allodesmus kernensis* holotype and Sharktooth Hill bonebed sample of *Allodesmus* mandibles (in cm unless indicated otherwise).

	Bonebed mandibles			*A. kernensis* type		
	OR	M	S	X	d	d/S
Length alveolar row, $C-M_2$	10.5-14.6	13.0	1.45	14.1	1.1	0.75
Length of symphysis	6.8-11.5	8.2	1.34	9.5	1.3	1
Breadth of symphysis	2.3-3.5	2.8	0.34	4.2	1.4	4.1
Angle, symphysis-alveolar row	35°-46°	41°	3.5°	45°	4°	1.2
Anteroposterior dia. alv. M_1	0.8-1.7	1.3	0.28	1.9	0.6	2.1
Length P_4-M_1 septum	0.3-1.2	0.6	0.25	0.1	0.5	-2.0

In the relative positions of the medial and lateral incisors, I can see no diagnostic differences between CAS 2472 and any bonebed mandible. Alveolar rims are complete in the former and incomplete in LACM 4320, and the completeness varies throughout the bonebed sample. Precise locations of these teeth are variable, as they are crowded next to the symphysis. In all mandibles the medial incisor is situated diagonally posteromedial to the lateral incisor.

Absence of a P_4-M_1 diastem in CAS 2472 is one of the marked differences between that mandible and two-thirds of the bonebed mandibles. In the sample, the diastem is variably developed, but in no other mandible is it as pronounced as in LACM 4320. In all mandibles, including the holotype of *A. kernensis* (CAS 2472), the P_4-M_1 septum is one of the largest in the cheek tooth series (fig. 3). In the total sample, thicknesses of other interalveolar septa and the condition of the molars are variable. Absence of a diastem in CAS 2472 cannot be considered a unique quality in light of the variable nature of the dentition in bonebed *Allodesmus*.

Mitchell stated that a sharp lateral flange is seen on the ascending ramus in LACM 4320 and not in CAS 2472. On LACM 4320, the anterior border of the coronoid process is flattened and expanded. On UCMP 81708 the anterior border of the coronoid process is narrow and smoothly rounded. The significance of such a flattening in some Allodesmus is unknown. The holotype of A. kernensis (CAS 2472) has the ascending ramus broken above the alveolar row, and the structure in question is not preserved.

Mitchell (1966, p. 34) noted that the symphysis of CAS 2472 "is more rounded and makes less of an angle with the axis of the ramus". The ventral portion of the symphysis of CAS 2472 is missing from its widest point to the genial tuberosity (fig. 3a) and has been missing since Kellogg described the specimen in 1922. Therefore, the overall shape of the symphysis is not discernible. The portion of the symphysis preserved is wider than that of any bonebed mandible included in this study. The angle between the symphysis and the alveolar row of CAS 2472 is close to 45°, which is near the upper limit of this measurement in bonebed mandibles (35°-46°).

The canine of CAS 2472 is nearly complete, but that of LACM 4320 is damaged. Therefore, differences in the emergence of this tooth from the two mandibles may be a factor of preservation. Emergence of the canine in CAS 2472 is like that in CAS 4487 or UCMP 81708. However with age, wear, and injury, the position of the canine in old individuals of living species may be altered.

Mitchell noted that alveolar septa of the holotype of A. kernensis are thinner and its alveoli relatively larger than in LACM 4320. One-half the bonebed mandibles resemble the holotype of A. kernensis in this respect more than they do LACM 4320.

A comparison of the holotype of A. kernensis with statistical data on the Sharktooth Hill bonebed sample of Allodesmus (Table 5) reveals that most of its dimensions lie within the observed range of the latter; half are near the standard deviation of the sample. Those exceeding the range of the bonebed sample reflect the large size and apparently extreme individual age of the holotype.

The holotype of A. kernensis (CAS 2472) cannot be excluded from the range of morphological characters seen in Sharktooth Hill bonebed mandibles of Allodesmus. The magnitude of variation is not discordant with that observed in a sample of a subspecies of living Otariidae. I therefore assign all the Allodesmus material from the Sharktooth Hill bonebed studied herein to the species A. kernensis Kellogg, 1922.

There are no conclusive arguments that the holotype of *A. kernensis* was collected from some formation other than the Round Mountain Silt. Caution should be exercised in drawing conclusions concerning that specimen, for it is damaged. It is also the largest of the known *Allodesmus* mandibles and may have belonged to an old male in which secondary characteristics may mask those diagnostic in younger specimens. Marine mammals are notoriously variable, and features used to diagnose taxa should be carefully chosen while at the same time utilizing large samples when available.

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PALEOBIOS

Contributions from the University of California
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No. 11 January 30, 1971

IMAGOTARIA (MAMMALIA: OTARIIDAE) FROM THE LATE MIOCENE SANTA MARGARITA FORMATION NEAR SANTA CRUZ CALIFORNIA

by

Lawrence G. Barnes

IMAGOTARIA (MAMMALIA: OTARIIDAE) FROM THE LATE MIOCENE SANTA MARGARITA FORMATION NEAR SANTA CRUZ, CALIFORNIA

by Lawrence G. Barnes

ABSTRACT

Fossil jaws and skull fragments of one individual referable to the extinct otariid genus Imagotaria have been recovered from the Santa Margarita Formation near Olympia in Scotts Valley, Santa Cruz County, California. The specimen supplies additional information on the anatomy of Imagotaria and extends the known geographic range of the genus 200 miles northward from the type locality of I. downsi in Santa Barbara County. Because of differences in the dentition, the new fossils cannot be referred confidently to I. downsi and may represent a more primitive form identified herein only as Imagotaria sp.

INTRODUCTION

One of the most recently proposed taxa of extinct sea lions or related animals (family Otariidae) is Imagotaria downsi Mitchell, 1968. The genus formed the basis for a new otariid subfamily, the Imagotariinae Mitchell, 1968. I. downsi is indeed a strange animal that possessed a combination of characters, some primitive and some advanced. The species is incompletely known from fragments of skulls, jaws, and postcranial bones from late Miocene or early Pliocene sediments near Lompoc, Santa Barbara County, California and supposedly related forms occur in deposits of comparable age in Orange County and Los Angeles County, California. A closely related animal has been found in late Miocene rocks in Santa Cruz County, California. This specimen consists of two jaws, teeth, and skull fragments and supplements knowledge of the anatomy of the mandible of Imagotaria.

ACKNOWLEDGEMENTS

I am grateful to Miss Linda Wong of Santa Cruz and to Mr. Clifford Nelson of the Department of Paleontology, University of California for their assistance in acquiring the specimen here described. I thank Mr. Charles A. Repenning of the U.S. Geological Survey for criticizing the manuscript and for allowing me to study material in his care. Mr. David Cook, staff artist of the Museum of Paleontology, University of California, prepared the line drawings.

METHODS

Measurements of the mandible were obtained in the manner outlined in a previous paper (Barnes, 1970). Abbreviations used in text are: UCMP-University of California Museum of Paleontology, Berkeley, California; SBMNH-Santa Barbara Museum of Natural History, Santa Barbara, California; UCMP V-prefix for UCMP vertebrate locality number; mm-millimeter; cm-centimeter; C-canine; I-incisor; M-molar; P-premolar.

SYSTEMATICS

Genus IMAGOTARIA Mitchell, 1968

Imagotaria sp.

Referred specimen: UCMP 88459: horizontal ramus of left dentary lacking coronoid and condyloid processes with imperfectly preserved C and P_{2-4}, right dentary lacking anterior end and parts of the coronoid process, tip of the crown of a canine tooth, a small fragment of the glenoid fossa of the right squamosal, and a fragment of the right jugal.

Locality: UCMP V-70184, Santa Cruz County, California, about 120 feet from the top of the Granite Rock Company quarry at 571 Quail Hollow Road, about one-half mile northwest of the community of Olympia in a valley just north of the center of Section 10, T 10 S, R 2 W, 37° 04' 40" north latitude and 122° 04' 00" west longitude, Felton, California 7.5' topographic quadrangle, U.S. Geological Survey, 1955 edition.

Formation and age: The specimen was found in a silty, gray, somewhat indurated sandstone in the Santa Margarita Formation of latest Miocene age. Reinhart (1959) and Mitchell and Repenning (1963) reported sirenians and desmostylians from the Santa Margarita formation not far from UCMP V-70184, and the latter gave a recent account of the geological setting.

Collector: Collected about 20 November 1968 by Mr. James Dumford.

DESCRIPTION

Dentary: The dentaries are the most important parts of this specimen. They resemble most closely the mandible of the holotype of *Imagotaria downsi* Mitchell, 1968, but are smaller. UCMP 88459 probably represents a juvenile individual, and the holotype of *I. downsi* (SBMNH 342) represents an adult (Mitchell, 1968, p.1844). The following features of UCMP 88459 indicate an immature animal: preserved enamel portions of the teeth do not show any indication of wear; the cheek teeth are crowded together; the mandibular symphysis is not very rugose; the canine tooth is incompletely erupted.

Mandibular characteristics (heavy anterior part and slender posterior region, rhomboid-shaped symphyseal surface, concave ventral margin of the horizontal ramus, shallow masseteric fossa, and cheek teeth with lingual cingulae) agree with Mitchell's description (1968, pp.1847-1849) of the holotype of *Imagotaria downsi*. The canine similarly has a posterior crista and rugose enamel surface. The medial incisor is diagonally posteromedial to the larger lateral incisor in UCMP 88459 as Mitchell suspected to be the case in *I. downsi*. Only two incisors exist. Two large mental foramina are present on the lateral surface of the dentary ventral to P_2, although Mitchell noted three in SBMNH 342. Small mental foramina ventral to the incisors number two as in *I. downsi*. The genial tuberosity is not as large as in the *I. downsi* holotype, probably because UCMP 88459 is a juvenile.

The entire number of mandibular teeth may be determined from UCMP 88459: I-2, C-1, P-4, M-1. A small procumbent medial incisor lies between the anterior part of the canine and the symphysis and is diagonally posteromedial to the larger lateral incisor which lies almost anterior to the canine. The tip of the canine is badly damaged, and the tooth is only partly erupted from the dentary. Its enamel margin is seen in lateral view where the alveolar rim is broken away. An isolated broken tip of another canine has a rounded conical apex with no wear surface.

Some cheek teeth of UCMP 88459 are distinctly two-rooted but such is not the case in *I. downsi*. In UCMP 88459 the cylindrical root of P_1 and the groove on the external surface of the single bilobed root of P_2 are as in SBMNH 342. P_{3-4} of *I. downsi* each has one root similar to P_2, but in UCMP 88459 each has two entirely separate roots as does M_1. The M_1 of *I, downsi* has two coalesced roots that diverge only at the extreme ends. An M_2 alveolus present in *I. downsi*

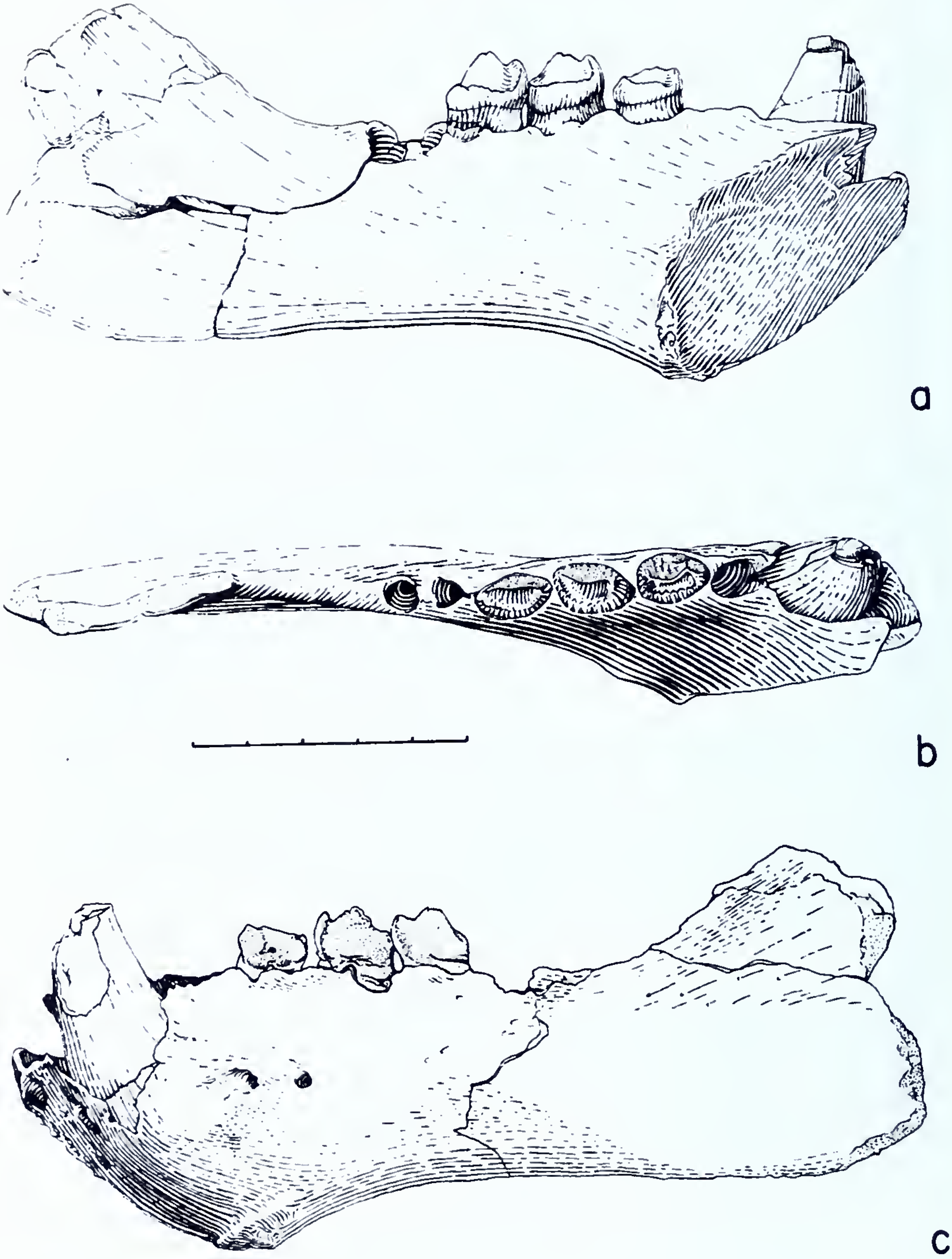

Fig. 1. Imagotaria sp., horizontal ramus of left dentary with canine and P_{2-4}, UCMP 88459, loc. V-70184; a, lingual view; b, occusal view; c, labial view. Scale line equals 5 cm.

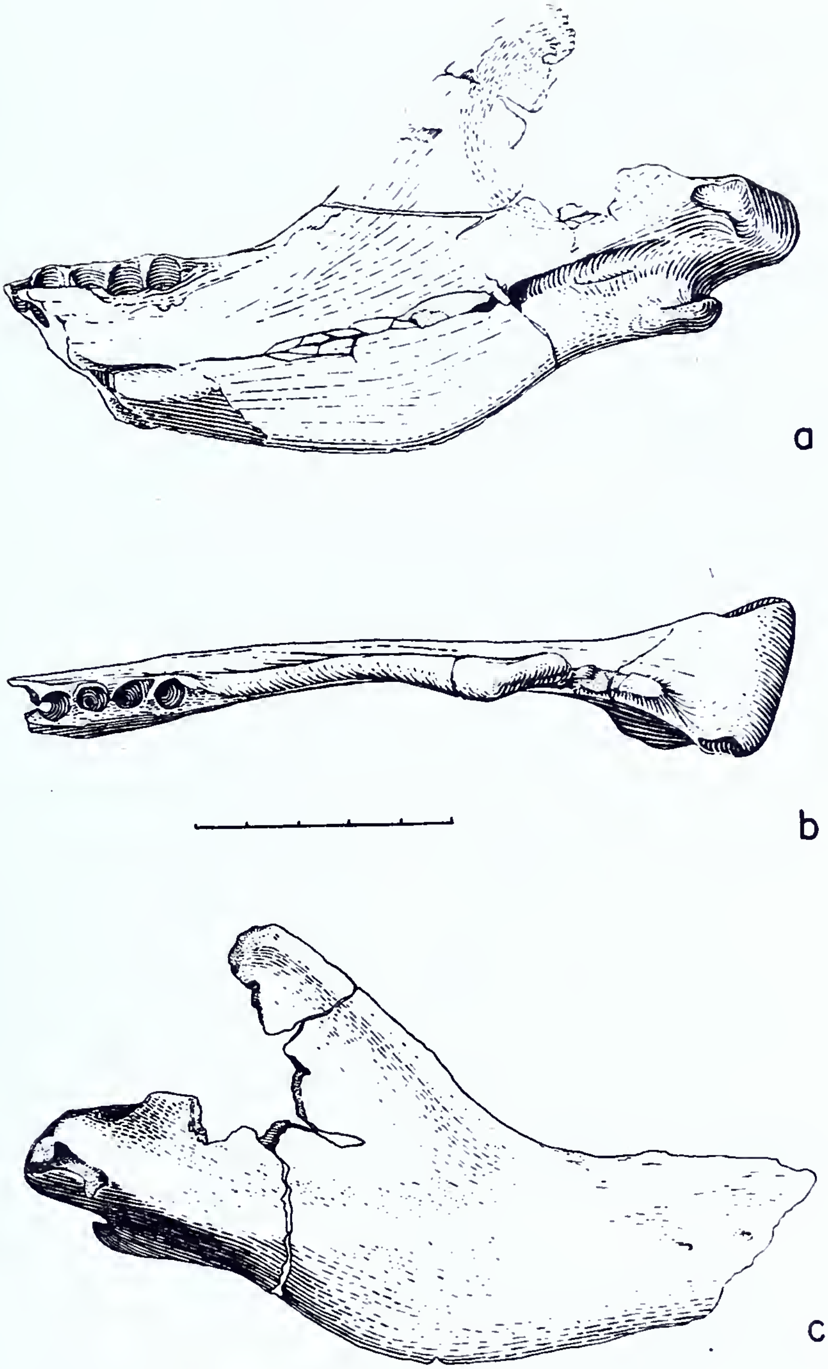

Fig. 2. *Imagotaria sp.*, posterior part of right dentary with alveoli for posterior root of P_3 and roots of P_4 and M_1, UCMP 88459, loc. V-70184: a, lingual view; b, occlusal view; c, labial view. Scale line equals 5 cm.

TABLE I. Measurements of Imagotaria mandibles, in mm.

	UCMP 88459	SBMNH 342
Total length, condyle to chin	(220)	----
Length of cheek tooth row, P_1-M_1	70.6	77.4
" " " " " , P_1-M_2	----	88.5
Length of symphysis	55.3	81.0
Breadth of symphysis	32.2	46.7
Depth of ramus at P_4	38.9	54.0
Anteroposterior diameter of alveolus of I_1	9.8	----
" " " " " I_2	10.7	----
" " " " " C	26.8	----
" " " " " P_1	10.1	10.1
" " " " " P_2	13.6	14.0
" " " " " P_3	15.8	16.0
" " " " " P_4	13.7	17.0
" " " " " M_1	14.8	14.6
" " " " " M_2	----	8.3
Greatest length of crown of P_2	13.0	13.0*
" " " " " P_3	14.9	15.0*
" " " " " P_4	15.0	----

( ) estimated measurement
* data from Mitchell (1968.)

is absent in UCMP 88459. Mitchell (1968, p.1847), noted variation in the presence or absence of this tooth in Recent Otariini and similar variation has been reported (Barnes, 1970, p.17) in a sample of *Allodesmus*.

P_{2-4} are preserved in place in the left dentary of UCMP 88459. Their lingual surfaces are well preserved, but their labial sides are weathered away. In gross anatomy the crowns of these teeth resemble their counterparts in I. downsi, and the anteroposterior length of the crowns of P_{2-3} are equal in the two specimens. The main central cusps are toward the labial side of the teeth, there are lingual cingulae, and P_{3-4} bear large anterior cingular cusps. No P_4 was preserved with SBMNH 342, but in UCMP 88459 P_4 is similar to P_3. Crowns of premolars of UCMP 88459 differ from those of I. downsi in that the lingual cingulae are more prominent and bear many small, distinct cingular cusps that are not obvious in the holotype of I. downsi.

The posterior part of the right dentary of UCMP 88459 is well preserved and displays characters not known in I. downsi. The dentary is thinnest below the coronoid process and has nearly flat internal and externol surfaces. As Mitchell stated, the masseteric fossa is extremely shallow and indistinct; on the inside of the coronoid process however, there is a well defined temporal fossa. The coronoid process is rather low with its apex located posteriorly and has a thick, rounded anterior margin rising very gently dorsoposteriorly from the level of the alveolar row. The condyloid process is located approximately level with the top of the alveolar row and is joined to the body of the dentary internally and externally by smooth, rounded struts. The large, tabular angular process located ventromedial to the condyloid process is directed posteromedially. The mandibular foramen is positioned low on the internal face of the dentary anterior to the angular process.

Squamosal: A fragment of the right squamosal forming the lateral part of the glenoid fossa is preserved. It suggests a large glenoid fossa about 30 mm in anteroposterior diameter with a heavy and rounded lateral extremity.

Jugal: The posterior extremity of the right jugal that extends ventral to the zygomatic portion of the squamosal is elongate and slender. There appears to have been no pronounced upward extension into a postorbital process.

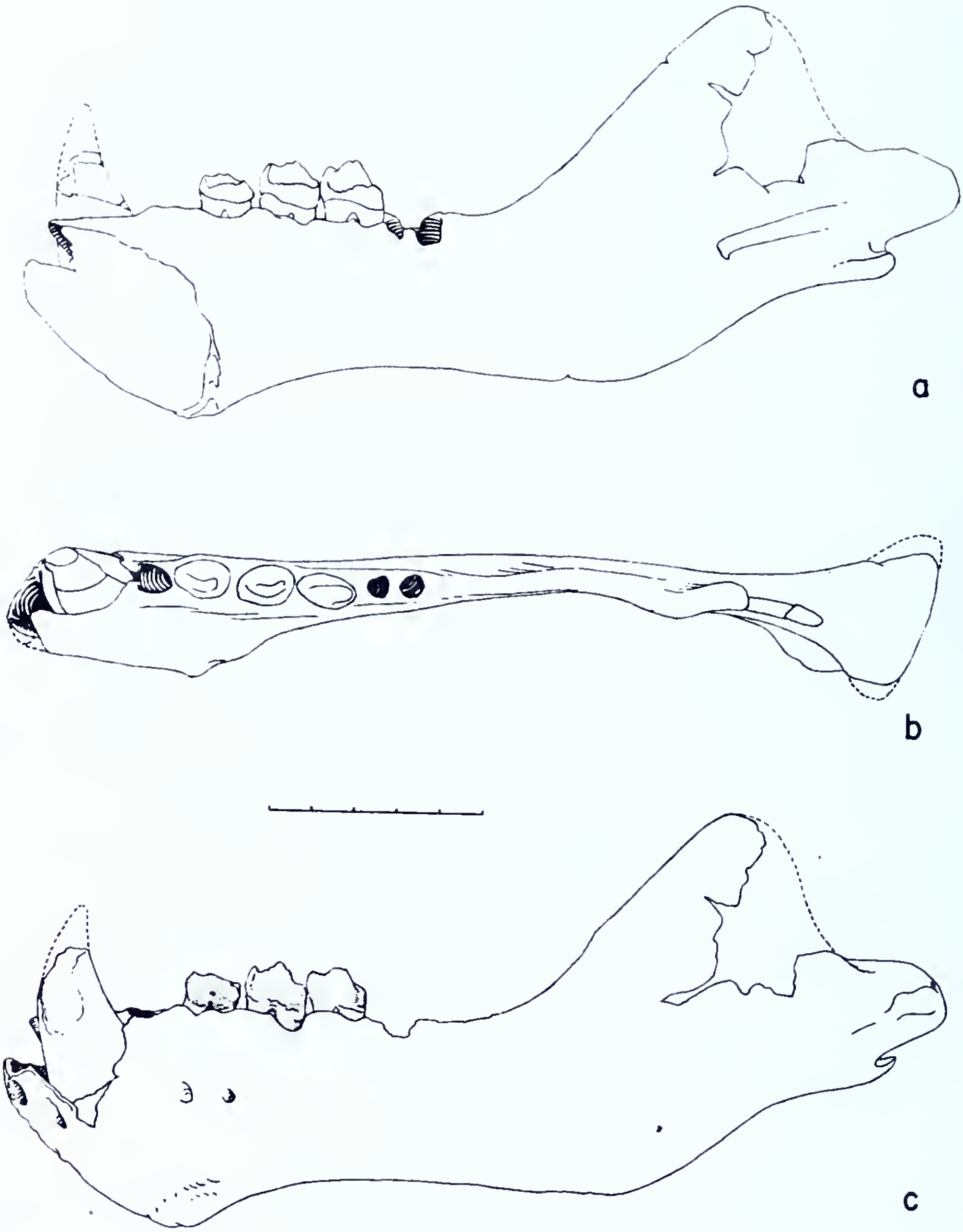

Fig. 3 *Imagotaria sp.*, composite restorations of right and left dentaries with canine and P_{2-4}, from UCMP 88459, loc. V-70184: a, lingual view of right dentary; b, occlusal view of right dentary; c, labial view of left dentary. Scale line equals 5 cm.

DISCUSSION

With the exception of some morphological differences attributable to the different individual ages of UCMP 88459 and the holotype of *Imagotaria downsi* (SBMNH 342), most features are sufficiently similar to allow UCMP 88459 to be identified as *Imagotaria*. The size of teeth are identical. An alveolus for a small single-rooted M_2 is present in SBMNH 342 and not in UCMP 88459. This may be of taxonomic importance or may be attributable to individual variation as discussed above. The most striking difference is that P_{3-4} and M_1 of UCMP 88459 are distinctly two-rooted, whereas these teeth in *I. downsi* have only faintly bilobed single roots. The difference may indicate the holotype of *I. downsi* is more highly evolved than UCMP 88459 in a supposed evolutionary process which would change a primitive multiple-rooted mammalian cheek tooth into a single-rooted type seen in such diverse, advanced pinnipeds as *Otaria*, *Eumetopias*, *Zalophus*, *Allodesmus*, *Odobenus*, *Halichoerus*, or *Mirounga*. Some living species of otariids show individual variation in the extent of cheek-tooth root coalescence, but it is not as extreme as the difference between UCMP 88459 and the holotype of *I. downsi*.

Another difference between the two specimens is the presence of a well developed lingual cingulum on cheek teeth of UCMP 88459. In *I. downsi* the cingulum is less prominent and less cuspate, but the difference is probably not very meaningful for the cingulae of SBMNH 342 may be reduced from wear. Because of differences in the cheek-tooth roots, I consider UCMP 88459 to be a more primitive species of *Imagotaria* and identify it as *Imagotaria sp.* at the present time.

Mitchell (1968) has dealt with the possible phyletic relationships of *Imagotaria* based mainly on cranial features. He theorized that the genus was derived from the Desmatophocinae as was the walrus subfamily, Odobeninae. One feature of the mandible supports this hypothesis: the position of the small medial incisor diagonally posteromedial to the larger lateral incisor. The same condition exists in the known mandibles of desmatophocines (sensu Barnes, 1971) and in the extinct odobenines *Alachtherium* and *Prorosmarus*, but it is very unlike the relatively more primitive condition that persists in Recent sea lions and fur seals (Otariinae), in which the two lower incisors lie side by side in a transverse plane. The low coronoid process and shallow masseteric fossa on the Imagotaria mandible are advanced features also seen in Dusignathus Kellogg, 1927, and some otariines.

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PALEOBIOS

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No. 12 March 30, 1971

CF. *UINTATHERIUM* (DINOCERATA, MAMMALIA) FROM THE UINTAN (MIDDLE TO LATE EOCENE) OF SOUTHERN CALIFORNIA

by

J. Howard Hutchison

no. 12

CF. *UINTATHERIUM* (DINOCERATA, MAMMALIA) FROM THE UINTAN (MIDDLE TO LATE EOCENE) OF SOUTHERN CALIFORNIA

By J. Howard Hutchison*

North American uintatheres were previously known only from the Rocky Mountain region (Wheeler, 1961). Recently two uintatheriid specimens, a fragmentary mandible and axis, were collected in sea cliff exposures about 50 feet above the beach and 1700 feet north of the shore terminus of the Scripps Institute Pier, La Jolla, San Diego County, California (32° 52' 15" N; 117° 15' 7" W), University of California Museum of Paleontology (UCMP) locality V-6874.

The fossils were imbedded in the sandstone part of a poorly consolidated marine clay clast conglomerate with an interstice matrix of medium grain sandstone. Milow and Ennis (1961) assign this unit to the cross-stratified siltstone-sandstone lens [Erc(d)] of the Rose Canyon Formation. The tongue is included within the *Amphimorphina californica* zone of the Ulatisian (Lutetian) foraminiferal stage.

Vertebrate specimens are broken and show evidence of pre-depositional abrasion. The two uintatheriid specimens were discovered about 100 feet apart but lay at about the same stratigraphic level and may represent a single individual. The axis was found in juxtaposition to an incomplete crocodilian jugal. The geology (particularly the lateral changes) and the included megafossils and microfossils led to the interpretation (Milow-in letter) that the site of deposition was a near-shore site, possibly on the flank and near the head of a deepwater submarine canyon or generally east-west submarine depression similar to those offshore the present beach. I conclude that the vertebrate remains were dumped into the canyon at the embouchure of a river.

The mandibular fragment (UCMP 82545) is broken or abraded on all its extremities but is not noticeably distorted (Figs. 1-3). M_2 is heavily damaged and only part of the posterior talonid crest remains (tooth terminology follows Wheeler, 1961). The preserved part of this crest lacks distinct cusps but has a beaded appearance. Main features of the M_3 are well preserved, but it is chipped on some extremities and moderately worn. The general morphology of the tooth agrees with figures and descriptions of Uintatheriinae (Wheeler, 1961). As in USNM 18603 (Pl. 13, Fig. 3 of Wheeler), the paraconid is "preserved very distinctly". The entoconid is indistinguishable from the rest of the beaded crest of the posterior loph. The posterior cingulum was apparently very short and weak. The condylar facet faces largely posteriorly as in other Uintatheriinae.

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*Contribution of the Museum of Paleontology.

In comparison to Tetheopsis speirianus (Osborn) 1881, the M_3 of UCMP 82545 is rather small but within range of M_3 lengths taken from published figures (Table 1). The "row of partially discrete, tiny cusps" on the posterior loph of the M_3 resembles that noted on PUM 10385 by Wheeler, but the cusps are apparently weaker. The only figured mandible of Tetheopsis which preserves the angular process (Osborn, 1881, Pl. 1, and Wheeler, 1961, Pl. 2, Fig. 1) does not have a strong emargination between the condyle and angular process, this area is broadly rounded in Osborn's figure. Wheeler's figure of the type skull of "Tinoceras stenops March" appears to indicate damage or restoration in this area. The dentary of Tetheopsis ingens (Marsh) 1885 is unknown.

Jaws of Eobasilus cornutus (Cope) 1872, figured by Cook (1926) under the name of Uintacolotherium blayneyi, show a rounded angular process and rather broad subcondylar emargination; although I have difficulty in seeing from the figure how much of this region was restored. M_3 of UCMP 82545 is smaller than that of Eobasileus measured by Cook.

Compared to molars of Uintatherium as defined by Wheeler (1961), the M_3 of UCMP 82545 is one or two millimeters larger than USNM 18603, which Wheeler (p. 47) characterized as "larger than average". The anterior emargination below the condyle and concomitant protuberancy of the angular process agree well with specimens Wheeler referred to Uintatherium anceps.

The axis, UCMP 88223, lacks part of the right side of the centrum, posterior epiphysis, neural arch and most of the transverse processes. The remaining body agrees well in all details with the axis of Uintatherium anceps illustrated by Marsh (1885, Pl. 21).

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TABLE 1

Comparison of M_3 length of San Diego specimen with other Uintatheriinae

Taxon	Length	Mus. No.	Source
Cf. *Uintatherium*	41.8mm	UCMP 82545	This paper
Tetheopsis speirianum	51.5*	YPM 11043	Marsh, 1885, Figs. 36-37
	47.5	YPM 11256	Marsh, 1885, Fig. 38
	44*	YPM 11567	Marsh, 1885, Fig. 47
	47	PUM 11611	Osborn, 1881, p. 31
Uintatherium anceps	40.3	USNM 18603	Wheeler, 1961, Pl. 13, Fig. 3
	37	YPM 11212	Marsh, 1885, Pl. 8, Figs. 1-2
	39	YPM 11039	Marsh, 1885, Pl. 19, Fig. 2
Eobasileus cornutus	45	CMNH 495	Cook, 1926, p. 11
	50*	CMNH 496	Cook, 1926, Pl. 2

*Approximate.

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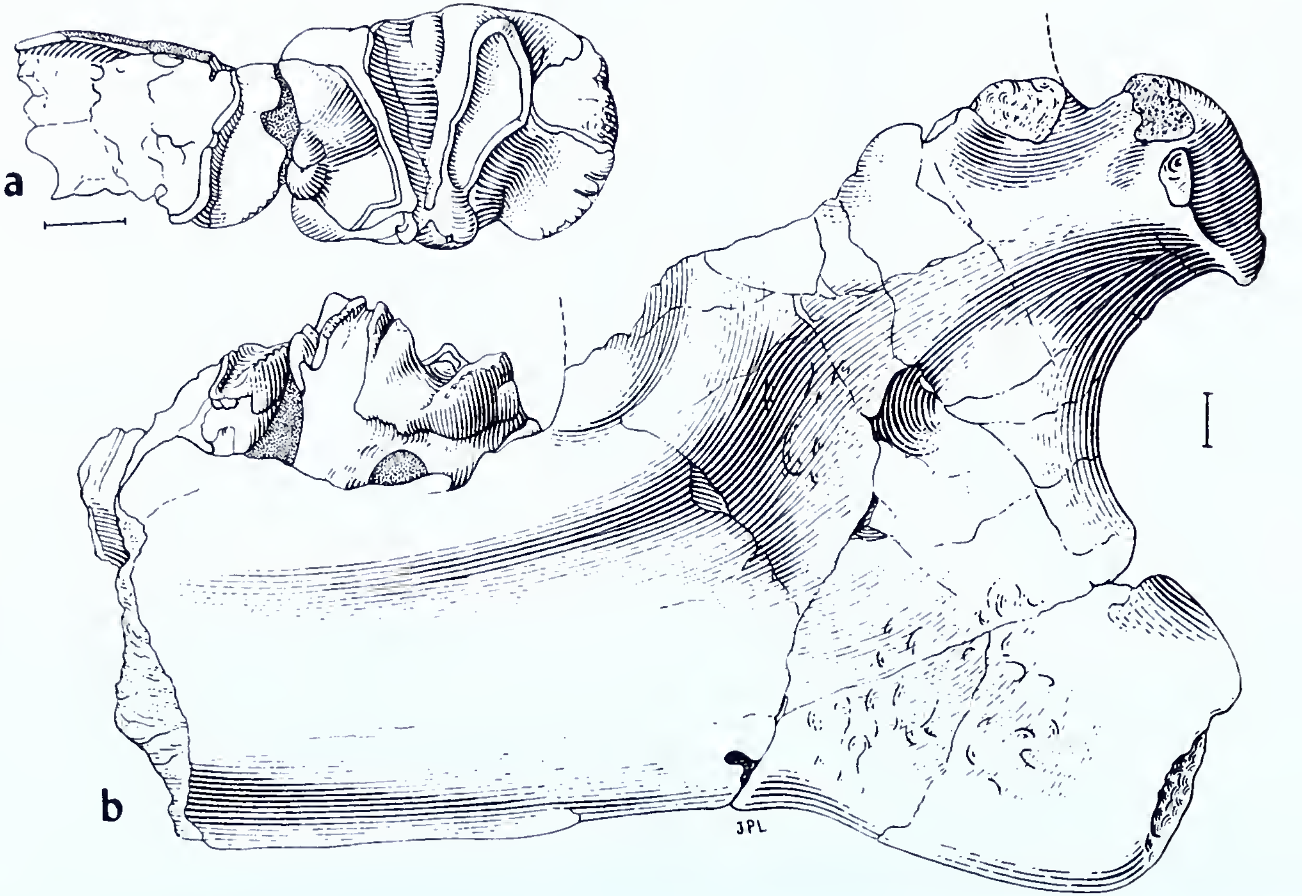

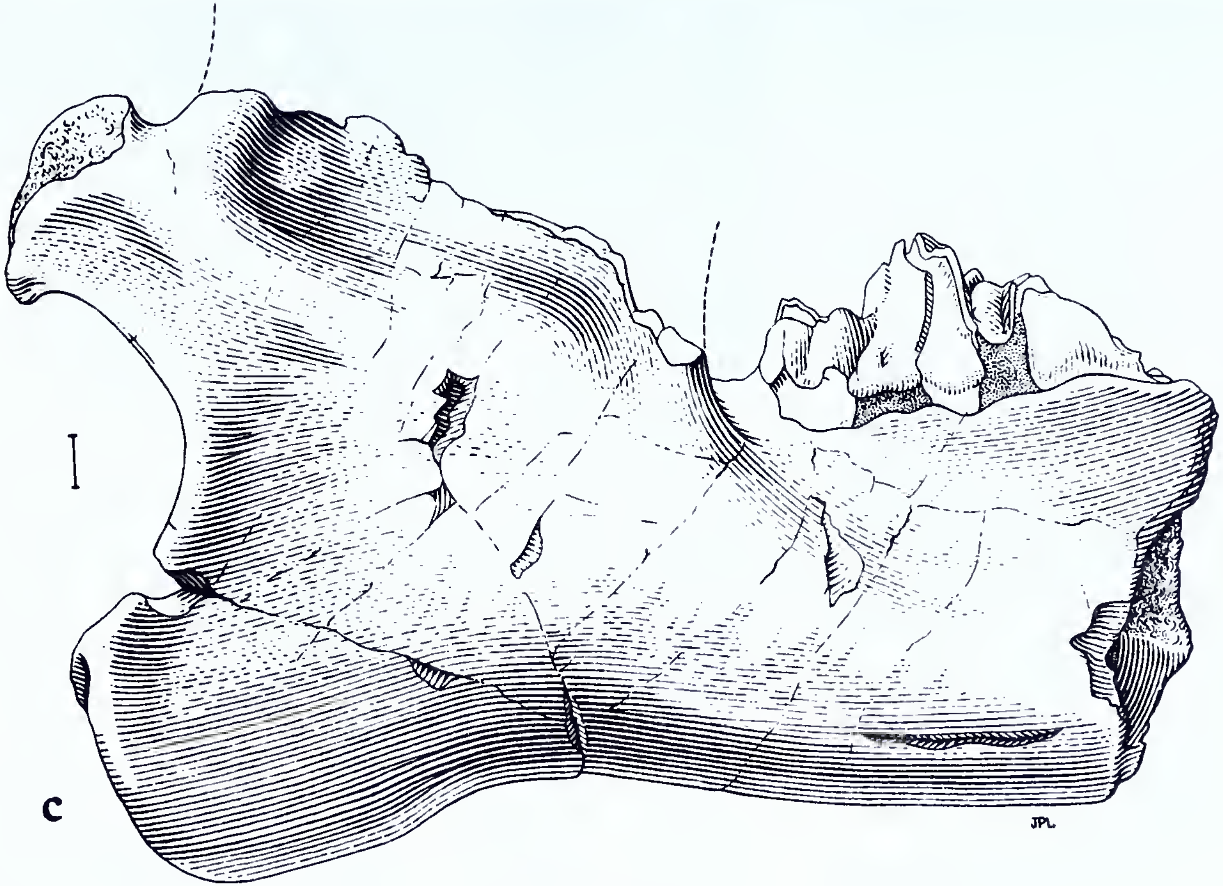

Fig. 1. Cf. *Uintatherium*, UCMP 82545, Rose Canyon Fm., UCMP Loc. V6874.
a. Occlusal view of incomplete M_2-M_3. b. Lingual view of dentary.
c. Labial view of dentary. (Scale line - 1 cm.)

no. 12

TABLE 2

Measurements of the axis UCMP 88223 following Marsh 1885

Length of axis along neural canal (posterior epiphysis absent)	118mm
Length of odontoid process	44
Transverse diameter of odontoid process	31
Vertical diameter of odontoid process	41
Transverse diameter of articular face of odontoid process	30
Anteroposterior diameter of articular face of odontoid process	31
Transverse (oblique) diameter of left anterior articular face	46
Vertical diameter of left anterior articular face	37
Transverse diameter across anterior articular faces, estimated	107
Distance between anterolateral articular faces	38
Transverse diameter of neural canal, estimated	37

Wheeler (1961) characterized *Uintatherium anceps* (genus monotypic) as a very variable species, and nothing in the morphology of UCMP 82545 and UCMP 88223 excludes them from the published concept of the species. However, lack of diagnostic material (i.e. skull) of the Californian species and small samples of *Tetheopsis* and *Eobasileus* necessitate only a provisional assignment of this material to *Uintatherium*.

An isolated tooth, LACM 21267, from Los Angeles County Museum of Natural History (= California Institute of Technology) locality 249 (subsite S) also seems referable to the Uintatheriidae and probably, because of its size, to the Uintatheriinae. The tooth is extremely worn (Fig. 2) but agrees in preserved details with a left M_1 or M_2 of a uintatheriid. Locality 249 and its fauna were described by Stock (1937, 1938), Wilson (1940a,b,c), Gazin (1955, 1958), and others and were considered as part of the Poway Formation. Milow and Ennis (1961) separated the actual fossil bearing beds below the Poway conglomerates as an unnamed formation overlying the Rose Canyon Fm. This unnamed unit is correlated with the upper part of the Ulatisian foraminiferal stage, although the facies at this locality is apparently fluviatile. Brattstrom (in Milow and Ennis, 1961, p. 30) raised some doubt about the exact location of locality 249 in the section but preservation of bones and surrounding matrix from this locality are identical to recent collections of bones immediately below the conglomerates of the Poway.

Mrs. J. P. Lufkin, the Museum staff artist, prepared the illustrations.

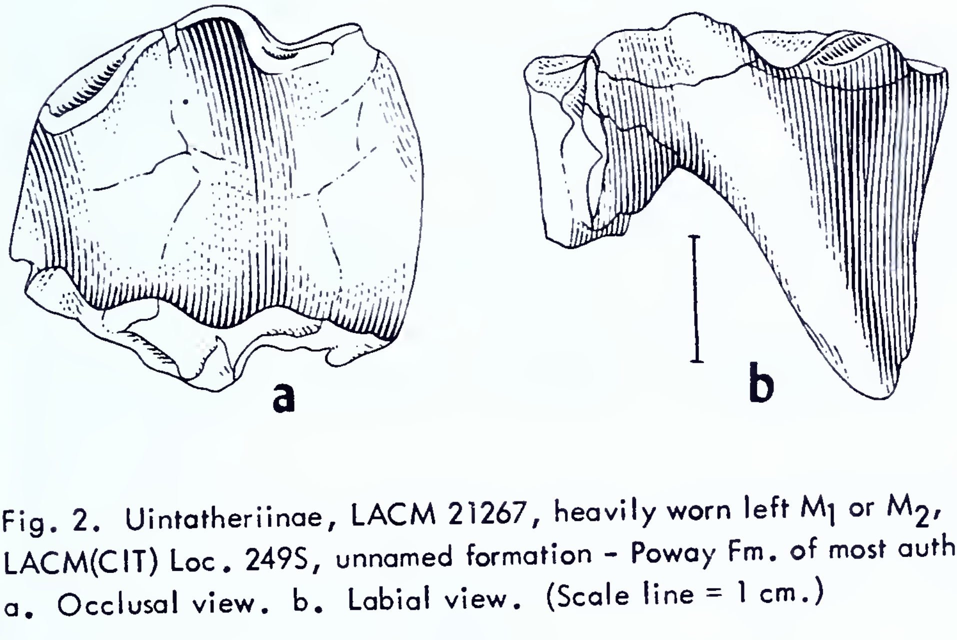

Fig. 2. Uintatheriinae, LACM 21267, heavily worn left M_1 or M_2, LACM(CIT) Loc. 249S, unnamed formation - Poway Fm. of most authors. a. Occlusal view. b. Labial view. (Scale line = 1 cm.)

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PaleoBios

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No. 13 September 30, 1971

A PLIOCENE COLUBRID SNAKE (REPTILIA: COLUBRIDAE) FROM WEST-CENTRAL NEVADA

by

John Ruben

no. 13

A PLIOCENE COLUBRID SNAKE (REPTILIA: COLUBRIDAE) FROM WEST-CENTRAL NEVADA

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ABSTRACT

An articulated, but incomplete, fossilized snake, from the middle member (approximately Middle Pliocene) of the Truckee Formation of west-central Nevada is Coluber sp. Linnaeus, 1758 (Reptilia: Colubridae). The specimen's original overall body length, about 830 millimeters, indicates that the serpent was about two years old and sexually mature at the time of its death. Presence of three fossilized fishes (at least one of which is Gasterosteus doryssus Jordan, 1907) within the rib cage of the specimen gives evidence that: (1) just prior to its death, the serpent maintained a summer home range that bordered on, or surrounded, a lake or stream; (2) the serpent was feeding on small fish shortly before it died (this the first recorded instance of Coluber consuming fish); (3) the specimen may have died as a result of its inability to properly swallow, or regurgitate, one of the fish; (4) the specimen probably died during the northern summer season.

INTRODUCTION

In the summer of 1969, Stephen Bruff and Bill Rowan, students at the University of Nevada, Reno, Nevada, discovered a partial skeleton of a colubrid snake, Coluber sp. Linnaeus, 1758, from the middle member (Hemphillian, approximately Middle Pliocene) of the Truckee Formation.

The specimen was found in a displaced slab of diatomite from the Eagle-Picher Quarry, which is in the Virginia Range (Fig. 1), about five miles southwest of Hazen, Nevada, in SE 1/4, SE 1/4 Sec. 12, T. 19N., R. 25E., Two Tips Quadrangle (USGS, 1957 ed.), Lyon County, Nevada (39°31'16"N; 119°07'07"W).

The serpent is the first recorded from the Truckee Formation, and along with Gasterosteus doryssus Jordan and Fundulus nevadensis Eastman, comprise the only known vertebrates from the middle member of the formation.

Because of its incompleteness, the fossilized snake offers only limited osteological comparison with Recent serpents but is of interest because articulated, fossilized ophidians are rare and because it contains within its rib cage the remains of three fish.

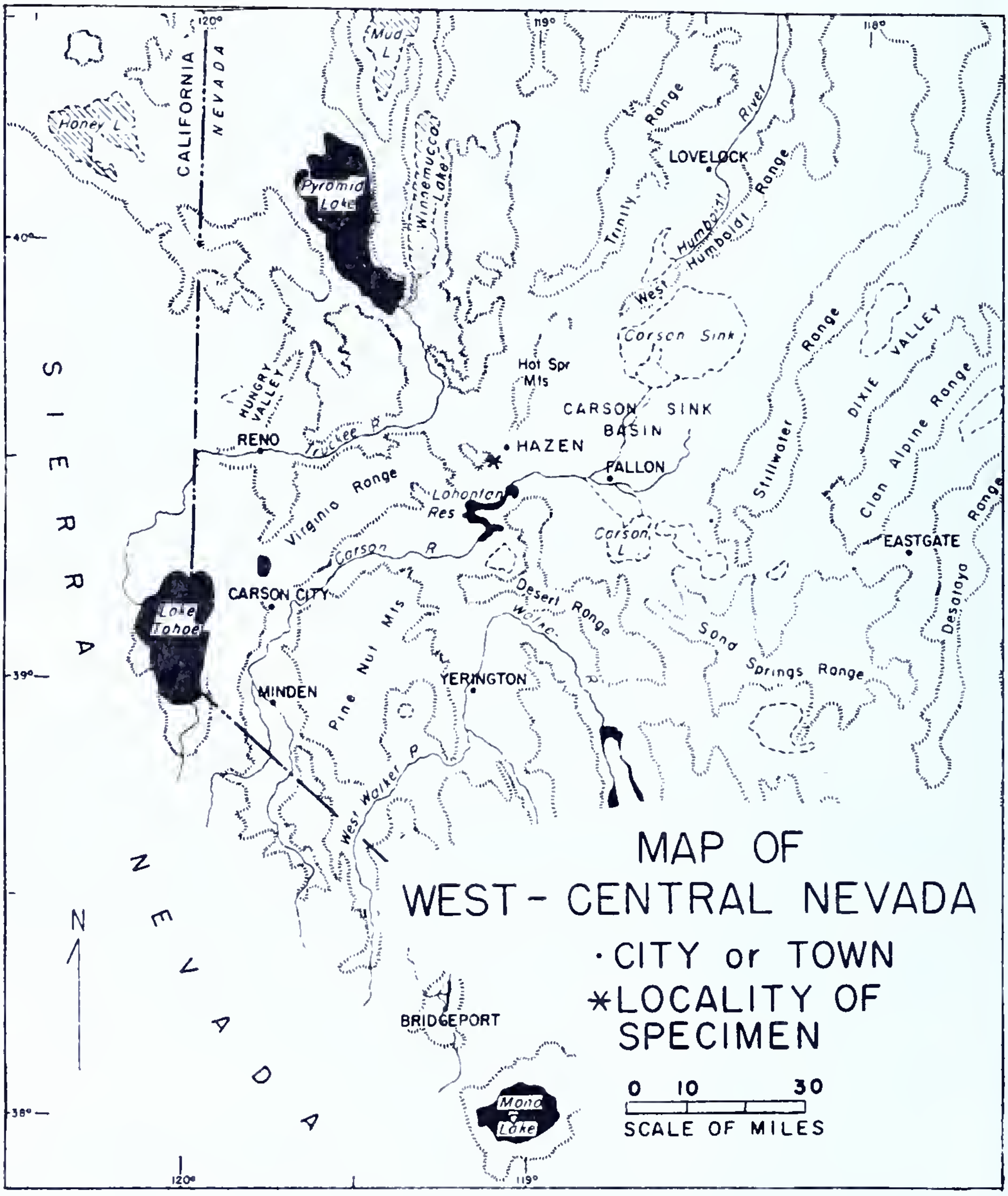

Figure 1. Geographic location of the specimen (modified after Axelrod, 1956, fig. 1).

The genus Coluber is known from Miocene to Recent times in Europe, and Pliocene to Recent times in North America (Romer, 1966: 367) and is represented by living animals also in parts of Asia, North Africa, Central and South America, and in the East Indies.

GEOLOGIC SETTING

King (1878: 412-423) first used the name Truckee Group for all sedimentary rocks in Western Nevada that he considered to be Miocene in age. In the same report he subdivided the Truckee Formation into eight members. Subsequent authors have shown the Truckee Formation to be Pliocene in age (see Fig. 2 and below), and Axelrod (1956: 101), after restudying the Truckee sediments and concluding that "... [King's] description of the formation is both misleading and inaccurate," devised the terms "Upper, Middle, and Lower" Truckee members. I shall follow Axelrod's terminology.

The 3350 feet of strata that comprise the Truckee Formation consist mainly of siliceous shales, sandstones, diatomites, and associated volcanic rocks. The middle Truckee Formation, in which the specimen was preserved, is as much as 1475 feet in thickness, and consists of soft, white diatomite, with thin pumice beds and a few thin, bluish-gray sandstone beds.

Fossilized mammals of Late Clarendonian age (Macdonald, 1956) have been found in the lower member of the Truckee Formation. Two fossil floras from the middle member of the formation are reported as Hemphillian in age (Axelrod, 1956, probably dated these floras on the basis of their stratigraphic position with respect to the Late Clarendonian mammals). The available fossil evidence thus indicates that the Truckee Formation extends from Early to Middle Pliocene in age. Axelrod has suggested that the upper member of the formation may be as young as late Pliocene (Early Blancan).

The middle Truckee diatomite deposits are tilted 10°-15° and unconformably overlain by horizontal Lake Lahontan (Quaternary) sediments. The diatomite was apparently deposited in a quiet, near-shore, slightly saline lacustrine environment (Schorn, 1970: pers. comm.) located in a region of mountain ranges and intermontane basins. Later movements and erosion have brought shifts in the boundaries of these basins and ranges as well as changes in the magnitude of the topographic features.

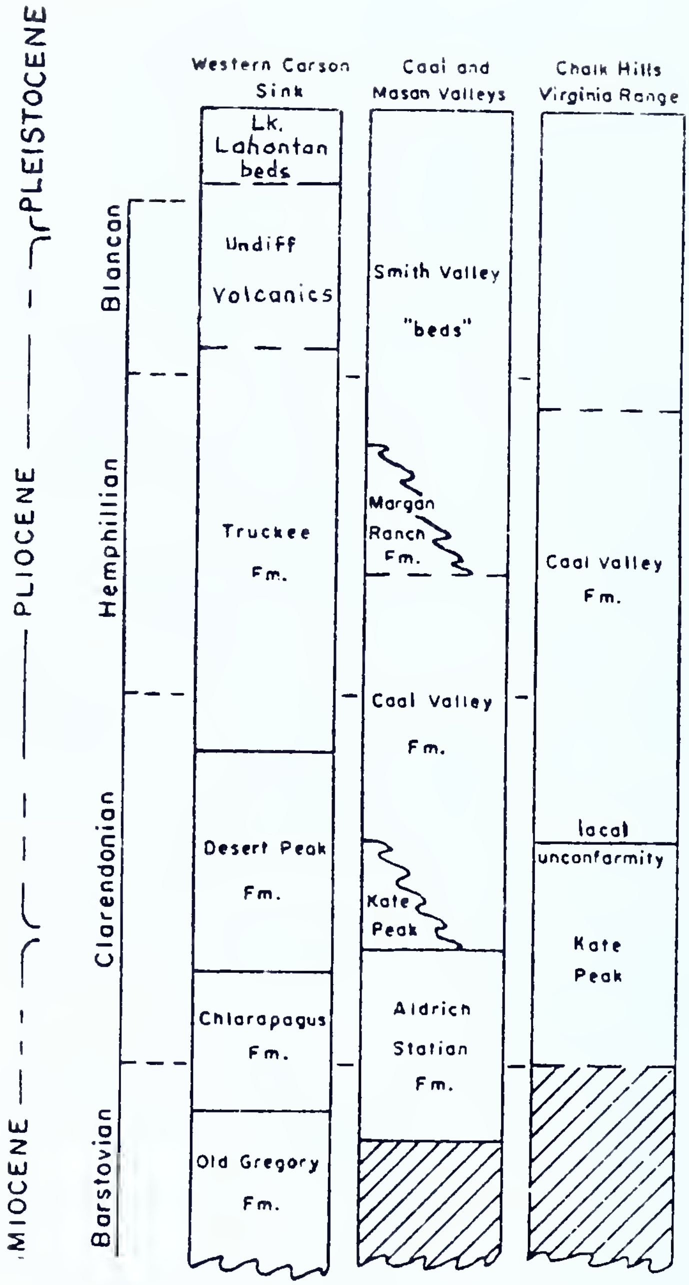

Figure 2. Stratigraphic sections of Mio-Pliocene rocks in western Nevada (modified after Axelrod, 1956, and Bonham, 1969).

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DESCRIPTION

Class REPTILIA
Order SQUAMATA
Family COLUBRIDAE
Subfamily COLUBRINAE
Genus COLUBER Linnaeus, 1758
Coluber sp.

Masticophis Baird and Girard, 1853.
Though *Masticophis* is considered by many neontologists to be distinct from *Coluber*, I could find no osteological criteria for separation of the genera.

The specimen, University of Nevada, Mackay School of Mines (UNMSM) 0001 (Fig. 3), which is firmly embedded in a diatomite slab, consists of an incomplete, partially articulated skull in position with the anteriormost (approx.) seventy-six vertebrae. The specimen, as preserved on the slab, lies with its dorsal aspect exposed, and when viewed from its left, is arranged in the form of a horizontally distended U-shape. Most of the ribs, or rib impressions, are present, though many are somewhat disarranged, particularly within the posterior fifth of the specimen. Remains of three fish are successively arranged within the rib cage, beginning at about the level of the thirty-second vertebra. The preserved section of the serpent is 260 millimeters long.

Dorsoventral crushing of the skull and jaws (Fig. 4) resulted in almost complete flattening and extensive breakage of these elements. The skull retains general ophidian proportions, but most bones of the braincase are either out of position or unrecognizable. Some palatal and jaw elements remain articulated or identifiable. Compared to Recent Colubrinae, the skull is of moderate size. Overall skull length = ±30mm.; skull width (distance between articular regions) = ±13mm.

The nasals are displaced laterally and lie with dorsal surfaces exposed and adjacent to the anterior portion of the right maxillary. A composite outline of the paired remains approximates an equilateral triangle with an apex at the posterior midline.

Six millimeters behind the nasals, a small displaced portion of the left frontal is visible in the region of the posterior braincase. Bone fragments, just posterior to the left frontal, may be remnants of the parietal bone.

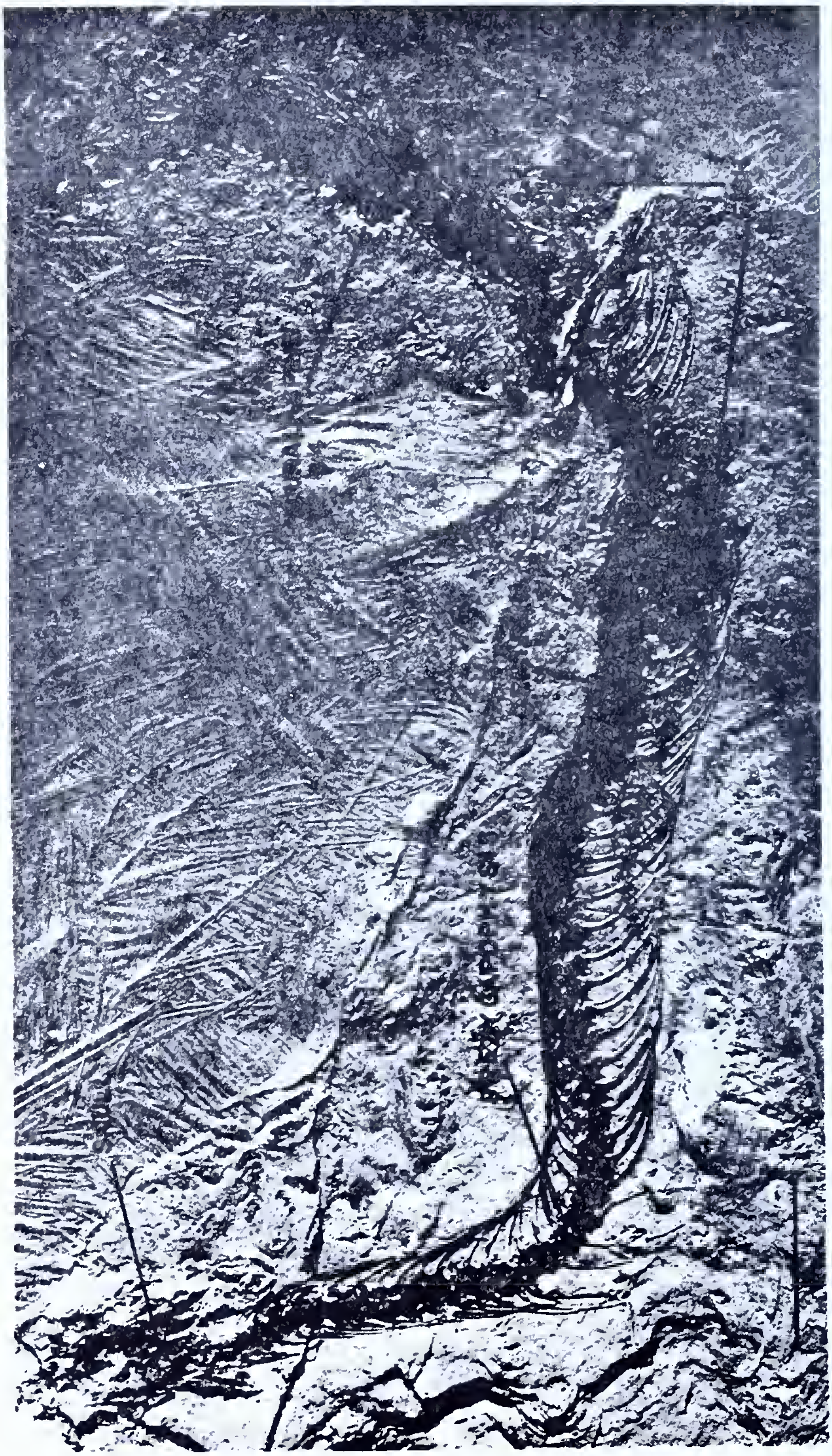

Figure 3. Coluber sp. UNMSM 0001 from near Hazen, Nevada. Dorsal view of specimen, anterior to left. Scale line equals 10mm.

The right supratemporal, a piece of fragmented, subtriangular bone, lies on edge, just internal to the posterior region of the right lower jaw.

Two small, randomly arranged elements, the anteriormost in the specimen, may be premaxillary fragments. The right maxillary lies on its lateral surface, posterolaterally to these fragments, and is adjacent to the nasals. Though laterally displaced about four millimeters, the right maxillary maintains generally normal spatial relationships to the rest of the skull. The maxillary is a slender, shaft-like element with eight teeth. Posteriorly, the bone is flattened in a nearly horizontal plane (in life). A short length of the posterior extremity and medial flange (that in life contacted the palatine bone) appear to be missing. Eight teeth (about one-half the total original number) and four alveolar spaces are present. The teeth are of moderate length, curved posteriorly at about a 50° angle to the maxillary, aglyphous and isodont. The left maxillary is unrecognizable or missing.

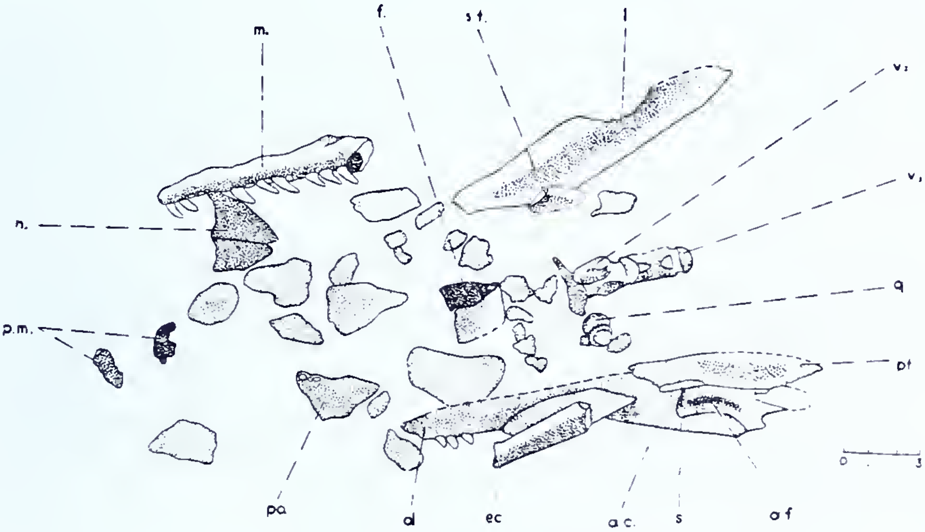

Figure 4. Coluber sp. Linnaeus, 1758. UNMSM 0001 from near Hazen, Nevada. Dorsal view of skull and two vertebrae (anterior to left). Abbreviations: a.c., left articular complex; a.f., adductor fossa; d., posterior region of left dentary; ec., left ectopterygoid (resting on fragment of pterygoid); f., left frontal; l., lateral wall of posterior region of right lower jaw; m., right maxillary; n., nasals; pa., left palatine; p.m., premaxillary fragments; pt., left pterygoid; q., articular facet of left quadrate; s., left stapes; st., right supratemporal; v2, axis; v3, vertebra #3. Scale line equals 3 mm.

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Identifiable palatal elements include parts of the left pterygoid, left palatine, and left ectopterygoid. All these elements are exposed dorsally.

A spool-shaped fragment, located about three millimeters posterolaterally from the left ectopterygoid, is tentatively identified as the articular facet of the left quadrate. Between the left pterygoid and adductor fossa of the left jaw is a short, dowl-like ossification that may be the left stapes.

Elements of both lower jaws are present and approximately in place. Much of the preserved part of the left ramus is overlain by the left pterygoid; however three posterior dentary teeth are visible. The remaining bones of the left articular complex are located external to the posterior region of the left pterygoid. The lateral wall of the adductor fossa and the adjoining anterior region are present. Lack of a separate coronoid indicates complete fusion of bones in this area.

Remains of approximately seventy-six vertebrae are present, or about the anterior 40% of the total original number of pre-cloacal segments. Inasmuch as most of these are embedded with ventral sides down in the block, a good lateral view is obstructed. Most neural arches and postzygapophyses are missing. Best preserved are vertebrae numbers nine through twenty-four. Generally there are only fragmented centra posterior to number twenty-four, hence an exact count of the number of vertebrae present in the specimen is difficult. No attempt has been made to precisely separate thoracic vertebrae into anterior or posterior sections (the posterior thoracic region generally begins at about segment 45). One cervical element, the axis, may be present.

Centra of the thoracic vertebrae are elongate (Table 1) with short-necked, posteriorly directed condyles. All thoracic centra bear two well developed epapophyses. These consist in each vertebra, of two separate ridge-like processes, superposed one behind the other upon the

Table 1. Centrum lengths, condylar widths, and ratio of centrum length to condylar width (=LCe/WCo) for vertebrae 67 and 70 of UNMSM 0001.

No.	Length Centrum	Width Contrum	LCe/WCo
67	4.32mm.	1.50mm.	2.88
70	4.31mm.	1.50mm.	2.88

floor of the neural canal. The posterior epapophysis tends to be longer, more acuminate, and more subtriangular. The impression in the matrix of the ventral surface of the seventy-fourth vertebra was exposed by carefully scraping away remaining bone fragments. Although I can make no definite statements regarding the conformation of the subcentral ridges, no hypapophysis exists at this point in the spinal column. The hemal keel is spatulate in shape.

Prezygapophyses tend to be obovate to oval in shape. The few accessory processes that remain appear to be well developed, acuminate, and directed anterolaterally.

One neural arch, that of the sixty-fourth vertebra, remains. The dorsal border of the spine is 2.38mm. long, and the height, measured from a level even with the top of the zygosphene, equals 0.97mm. There is a very slight overhang of the neural spine both anteriorly and posteriorly. The zygosphene appears slightly convex from above.

Most of the ribs retain their original shape and proximal association with their correlative vertebrae. However they now lie in a primarily horizontal plane with respect to the spinal column. The longest complete rib, which articulates with the thirty-ninth vertebra, is about 20mm. in length.

IDENTIFICATION

Because of the relatively recent date (Hemphillian) assigned to the sediments in which UNMSM 0001 was discovered, it seems likely that the specimen is at least generically identical to one of the extant kinds of serpents of North America, north of Brownsville, Texas (about lat. 26°N.). UNMSM 0001 is excluded from the Leptotyphlopidae on the basis of the poorly developed dentition, presence of a separate coronoid element and lack of an ectopterygoid in that family (for a more complete listing of leptotyphlopid characteristics, see Romer, 1956, p. 568).

The Boidae are eliminated from consideration by the proportions of their vertebrae, which are shorter and broader than those of UNMSM 0001. Inasmuch as the Crotalidae, Elapidae, and natricine Colubridae can also be eliminated because UNMSM 0001 lacks a hypapophysis on at least one pre-cloacal vertebra, the fossil is very likely one of the colubrine Colubridae.

Approximately thirty genera of colubrine snakes live within the geographic area under consideration. Of these, the following are immediately distinguishable from UNMSM 0001 on the basis of the following listed morphological characteristics:

Genus	Characteristic	UNMSM #0001
Abastor Gray	accessory process obtusely shaped and laterally directed (Auffenberg, 1963: 167)	accessory process acuminate and anterolaterally directed
Carphophis Gervais	ratio nlu/nh[1]=5.52-7.83 (*Ibid.*); maximum length =365mm. (Conant, 1958: 144)	ratio nlu/nh=2.46; length=830mm. (see "Paleoautecology")
Chilomeniscus Cope	opisthodont dentition (Stebbins, 1954:355); maximum length=245mm. (Stebbins, 1966: 178)	isodont dentition[2]; length=830mm.
Chionactis Cope	opisthodont dentition (Stebbins, 1954: 355); maximum length=431mm. (Stebbins, 1966: 176)	isodont dentition; length=830mm.
Coniophanes Hallowell	opisthodont dentition (Conant, 1958: 145); maximum length=508mm. (*Ibid.*)	isodont dentition; length=830mm.
Diadophis Baird and Girard	zygosphene crenulated dorsally (Auffenberg, 1963: 170; Holman, 1959: 100); maximum length=760mm. (Stebbins, 1966: 143)	zygosphene concave dorsally; length=830mm.

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[1] Auffenberg's (1963: 154) symbol for the ratio obtained by dividing the length of the dorsal border of the neural spine by the height of the neural spine.

[2] UNMSM 0001 lacks the posterior extremity of the right maxillary, hence absolute proof of complete isodonty is lacking. However, indirect evidence provided by the maxillary teeth present suggest an opisthodontous condition was absent; *i.e.* angle of teeth to maxillary in *Pituophis*, *Coluber*, and UNMSM 0001 is approximately 50°; in two specimens each of *Heterodon*, *Hypsiglena*, and one *Sonora*, the angle is approximately 25°.

Genus	Characteristic	UNMSM #0001
Drymarchon Fitzinger	anterodorsal edge of neural spine beveled (Auffenberg, 1963: 176)	anterodorsal edge of neural spine not beveled
Elaphe Fitzinger	nlu/nh=0.89-1.21 (Ibid.: 182)	nlu/nh=2.46
Farancia Holbrook	accessory process obtusely shaped and laterally directed (Ibid.: 176)	accessory process acuminate and anterolaterally directed
Ficimia Gray	opisthodont dentition (Stebbins, 1954: 355); maximum length=483mm. (Conant, 1958:.178)	isodont dentition; length=830mm.
Heterodon Latreille	opisthodont dentition (Stebbins, 1954: 355); median apex of nasals anterior	isodont dentition; median apex of nasals posterior (see "Description")
Hypsiglena Cope	opisthodont dentition (Stebbins, 1954: 355); maximum length=660mm. (Stebbins, 1966: 184)	isodont dentition; length=830mm.
Leptodeira Fitzinger	opisthodont dentition (Conant, 1958: 179)	isodont dentition
Opheodrys Fitzinger	nlu/nh=1.39-1.45 (Auffenberg, 1963: 175; Holman, 1962: 259)	nlu/nh=2.46
Oxybelis Wagler	opisthodont dentition (Stebbins, 1954: 355); ratio length skull/width skull=4.5 (see drawing, p. 453, Stebbins, 1966)	isodont dentition; length skull/width skull=2.3 (see "Description")
Pituophis Holbrook	nlu/nh=0.90-1.16 (Auffenberg, 1963: 183)	nlu/nh=2.46

Genus	Characteristic	UNMSM #0001
Rhadinia Cope	zygosphene crenulated dorsally (Auffenberg, 1963: 171; Holman, 1959: 100); maximum length=405mm. (Conant, 1958: 140)	zygosphene concave dorsally; length=833mm.
Rhinocheilus Baird and Girard . .	posterodorsal edge of neural spine with strong backward projection	posterodorsal edge neural spine lacks strong backward projection
Salvadora Baird and Girard . .	nlu/nh=1/54-1/58 (Auffenberg, 1963: 176)	nlu/nh=2.46
Sonora Baird and Girard . .	opisthodont dentition (Stebbins, 1954: 355); maximum length=482mm. (Stebbins, 1966: 175)	isodont dentition; length=830mm.
Tantilla Baird and Girard . .	opisthodont dentition (Stebbins, 1954: 355); maximum length=457mm. (Stebbins, 1966: 181)	isodont dentition; length=830mm.
Trimorphodon Cope	opisthodont dentition (Stebbins, 1954: 355)	isodont dentition

The ratio derived by dividing length of centrum (measured from anterior extremity of dorsal lip of the cotyle to the posterior extremity of the condyle) by condylar width (LCe/WCo), is also useful for identification. Such a ratio was obtained from each of 12-14 vertebrae selected at equal intervals (every tenth segment) from the posterior thoracic region[3] (those pre-cloacal vertebrae lacking hypapophyses) in each of seven articulated specimens of Pituophis melanoleucus, and two each of Arizona elegans, Coluber constrictor, C. lateralis, and

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[3] Segments 45-165 were sampled (posterior thoracic vertebrae beyond this point often tend to have inconsistent LCe/WCo ratios, as do anterior thoracic segments). In a few specimens the posterior thoracic region began anterior to 45. This accounts for any N > 12, since sampling was always carried to 165.

Lampropeltis getulus. When the mean LCe/WCo values from each individual are plotted against its correlative overall body length (table 2, fig. 5), two factors are immediately apparent: (1) with increase in overall body length, all genera show consistently greater LCe/WCo values; (2) vertebrae of A. elegans, L. getulus, and P. melanoleucus possess generally like LCe/WCo values for similar overall body lengths but exhibit consistently lower LCe/WCo values than do vertebrae from specimens of the genus Coluber with similar overall body lengths.

The average LCe/WCo value from posterior thoracic vertebrae of UNMSM 0001 (Table 1), plotted as a single point in Figure 5, lies close to the line of best fit for Recent Coluber. Arizona, Lampropeltis, and Pituophis differ significantly from UNMSM 0001 in this aspect.

Ratios derived by dividing centrum length by neural arch width (Auffenberg, 1963) in posterior thoracic vertebrae of Cemophora Cope, Drymobius Fitzinger, Elaphe, and Stilosoma Brown indicate these genera are similar in this aspect to Lampropeltis and Pituophis. Such ratios tend to separate Coluber sp. from the latter genera in a similar manner to that seen in LCe/WCo ratios. Therefore, I assume that LCe/WCo values for Cemophora, Drymobius, Elaphe, and Stilosoma would be similar to those of Lampropeltis and Pituophis.

UNMSM 0001 may also be distinguished from some of the previously mentioned genera by ecological criteria. Axelrod (1956: table 17) reports the Hemphillean environment of the Hazen area to have been basically a "Riparian occurrence for trees in semi-arid open grassland and scrub region [;] 12"-15" rain as summer showers, winter rains; cool winters." The Hazen flora includes Jamesia (Populus), Purshia, and Rhus (Axelrod, 1950: 244). These environmental conditions and floral taxa closely agree with those described for the Southern Oak Woodland plant community of Munz and Keck (1965: 16). Areas of Southern Oak Woodland, in turn, correspond to the Upper Sonoran life zone of Hall and Grinnell (1919: 51) and Grinnell (1935: plate 3). Inasmuch as UNMSM 0001 was almost certainly not an allochthonous element of the Hemphillian Hazen biota, I regard it as an Upper Sonoran animal. Chilomeniscus, Chionactis, and Phyllorhynchus Stejneger may be distinguished from the fossilized snake on the basis of their exclusively Lower Sonoran occurrence. Rhadinia and Farancia, serpents exclusively of tropical swamps and lowlands of the southeast U.S., may be likewise excluded.

Table 2. Ratios of centrum length-condylar width (=LCe/WCo) from fifteen specimens (four genera, five species) of Recent colubrine snakes (Univ. Calif. Museum of Paleontology). L, overall body length; N, sample size; O.R., observed range LCe/WCo (by extreme measurements); $\bar{X}$, mean; S.D., standard deviation.

Species	L	N	O.R.	$\bar{X}$	S.D.
Arizona elegans	419mm.	13	1.93-2.04	1.98	0.02
" "	938	12	2.19-2.29	2.23	0.03
Coluber constrictor	811	14	2.76-3.07	2.90	0.10
" "	1140	12	3.12-3.32	3.20	0.05
Coluber lateralis	660	13	2.61-2.96	2.73	0.09
" "	1093	13	3.06-3.28	3.16	0.06
Lampropeltis getulus	305	16	1.73-1.91	1.82	0.03
" "	1093	13	2.56-2.76	2.64	0.07
Pituophis melanoleucus	457	14	1.73-1.91	1.83	0.05
" "	481	12	1.99-2.14	2.07	0.03
" "	890	12	2.20-2.34	2.27	0.03
" "	940	12	2.22-2.40	2.33	0.04
" "	965	12	2.26-2.43	2.35	0.04
" "	1244	12	2.53-2.68	2.61	0.03
" "	1270	12	2.42-2.61	2.52	0.04

UNMSM 0001 is here assigned to the genus *Coluber* on the basis of similarity of nlu/nh ratio (*Coluber*=1.86-3.46; UNMSM 0001=2.46), LCe/WCo values, ecological similarities (range of *Coluber* includes the Upper Sonoran life zone), as well as the differences from other genera mentioned above. As the specimen cannot be confidently assigned to any particular species, I found no way to define its taxonomic position more precisely than to genus. Additionally, since other fossilized colubrids of equivalent age have been considered inseparable from living species, I see little criteria for erection of a chronospecies.

GASTROINTESTINAL CONTENTS

A fairly well preserved fish lies within the rib cage, beginning at about the level of the thirty-second vertebra. From this point, it extends posteriorly, parallel to the serpent's vertebral column, some 60mm. The fish lies on its left side with the head directed posteriorly in relation to the snake. Posterior to this, located at about the levels of the fifty-sixth and seventy-fourth vertebrae, are poorly preserved remains of two other fish. The poor condition of the two more posteriorly situated fish may be attributed to their having been subject to digestive processes. The remains of the two posterior fish are too poorly preserved to identify, but the anteriormost is tentatively identified as *Gasterosteus doryssus* Jordan.

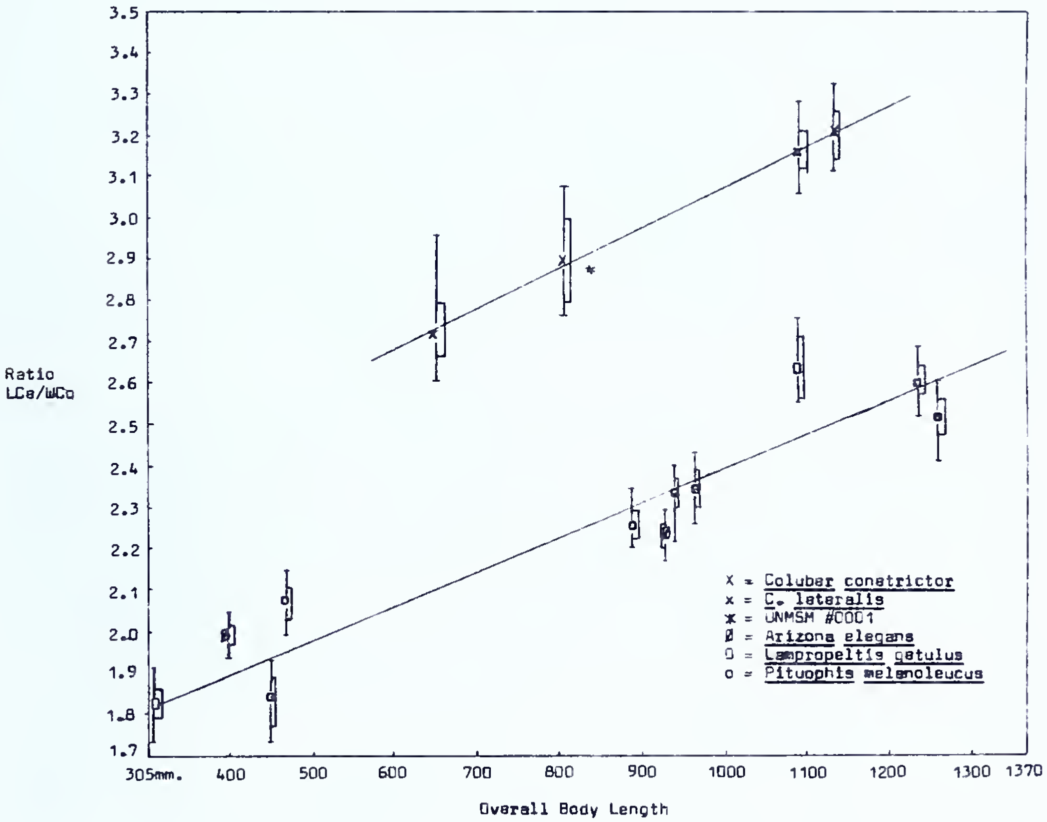

Figure 5. Allometric growth in posterior thoracic vertebrae (≃45-165) of four Recent colubrine genera (five species). Ratios of length of centrum to condylar width (=LCe/WCo) plotted against overall body length, data in Table 2. Abscissal and ordinate scales linear. Lines of best fit of the means arranged on the hypothesis that two distinct growth patterns occur. Each entry represents values of samples from one individual. Symbols are means. Vertical lines are observed ranges. Rectangles mark standard deviation. Asterisk represents mean ($\bar{X}$) of two vertebrae from UNMSM 0001 (Table 1). Length of UNMSM 0001 as estimated in Figure 6.

PALEOAUTECOLOGY

Knowledge of the length of the centrum from vertebra 70 (Table 1) makes possible a reasonable estimate of the overall body length of UNMSM 0001. Measurements of the centrum length of segment 70 from fifteen Recent colubrids (four genera, five species) were plotted against the corresponding overall body length of each individual. As seen in Figure 6, length of centrum in vertebra 70 is highly correlated with overall body length in most of the Recent specimens. Placed on its correct position on the line of best fit in Figure 5, the length of the centrum from vertebra 70 in UNMSM 0001 indicates the specimen's original length was equal to about 830mm.

This body length supports certain interpretations as to the age and condition of sexual maturity of UNMSM 0001 at the time of its death. Fitch (1963: 433) recorded lengths of Recent specimens of Coluber constrictor of different age groups. The estimated length of UNMSM 0001 falls within the two year age group as given by Fitch. Fitch reports Recent specimens of both sexes in this age bracket are sexually mature; I assume that at the time of its death, UNMSM 0001 was mature also.

The serpent may have died from its inability to properly swallow, or regurgitate, one of the fish contained in its gastrointestinal tract. Dissections of the gastrointestinal tract of Recent colubrids indicate that the cardiac sphincter of the stomach of UNMSM 0001 was probably situated at about the level of the sixtieth vertebra (±190mm. posterior to the snout). Inasmuch as the anteriormost of the three fish present is situated between the levels of the thirty-first (95mm. posterior to the snout) and the forty-eight (155mm. posterior to the snout) vertebrae, I believe that the fish in question was located in the snake's esophagous, rather than stomach, at the time of the serpent's death. The sharp dorsal spines possessed by Gasterosteus could easily have become lodged in the serpent's gullet in such a manner as to prevent further esophageal transport of the fish, thus causing the snake's death.

PALEOECOLOGY

That UNMSM 0001 was not alien to the Hemphillian Hazen environment is indicated by the presence of Gasterosteus doryssus, one of the previously reported genera from the Hazen diatomite deposits, in the digestive tract of the serpent.

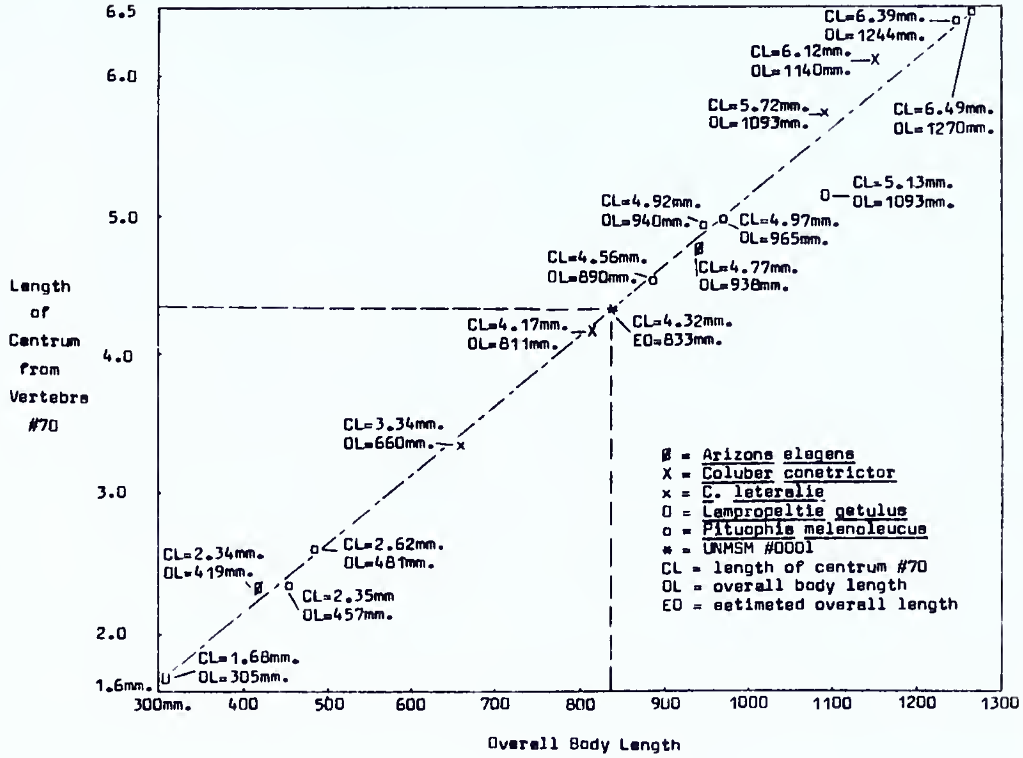

Figure 6. Length of centrum from vertebra 70 compared to overall body length in fifteen Recent colubrids (four genera, five species) and UNMSM 0001. Estimated overall body length of UNMSM 0001 based on the generally rectilinear relationship between increments in CL and OL in the fifteen Recent specimens.

Little can be added to the general description of that environment, as given on page 13. With respect to the lacustrine environment, Schorn (1970: pers. comm.) reports that the genera of diatoms present in the diatomite slab upon which UNMSM 0001 is preserved include Cymbella, Epithenia, and Surirella. These are indicative of slightly saline water conditions (Smith, 1950). Additionally, about 50% of the diatoms present were encysted at the time of deposition. Saline water conditions are here interpreted as having resulted from the semi-arid condition of the region, and the encysted state of many of the diatoms indicates that burial of UNMSM 0001 occurred during a particularly dry season, perhaps during the northern summer season.

The presence of fish, recently ingested prior to the death of UNMSM 0001, suggests that the serpent died during the northern summer season, inasmuch as hibernation began and feeding activity probably ceased during the cool winter season.

The snake's summer home range probably bordered on, or surrounded, the lake or stream from which the fish were obtained. Fitch (1963: 386) reports maintenance of stable summer home ranges, averaging 6.6 acres in area, by Recent specimens of Coluber constrictor.

This is the first recorded instance of any Coluber, fossil or Recent, having consumed fish.

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PALEOBIOS

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 14 December 29, 1972

MIOCENE MAMMALS, STRATIGRAPHY AND ENVIRONMENT OF MURUAROT HILL, KENYA

by

Cary T. Madden

MIOCENE MAMMALS, STRATIGRAPHY AND ENVIRONMENT OF MURUAROT HILL, KENYA

BY CARY T. MADDEN

ABSTRACT

Fossil mammals from Muruarot Hill in northwestern Kenya are conspecific with mammals in the Early Miocene fauna of Rusinga Island indicating that the age of the Muruarot Hill fauna, long disputed, is almost certainly Early Miocene. Analyses of the sediments and the gastropod and mammal faunal indicates that the paleoenvironment of the site was probably semi-arid and relatively open with shallow, swampy lakes.

INTRODUCTION

Miocene mammals were first described from Muruarot Hill, near Lodwar, in northwestern Kenya (Fig. 1) by the French paleontologist Camille Arambourg (1933). Arambourg compared nearly all of his fossils with similar mammals from the Burdigalian of Europe and concluded that they were more primitive, and therefore, somewhat older than their closely related European counterparts. He consequently placed his fauna in the earliest Burdigalian which was then usually considered to be the earliest subdivision of the Miocene Epoch (Davies, 1934). Since the time of Arambourg's report, fossil mammals have been recorded from Muruarot Hill by several workers (Deraniyagala, 1951; Whitworth, 1954, 1958; Savage, 1965; Hooijer, 1968; Churcher, 1970). Although most of the taxa recorded by these workers are generally considered to be characteristic of an Early Miocene age (see Table 1), and they thus tended to substantiate Arambourg's relative age determination, the age of the Muruarot fauna has nonetheless been disputed (see, for example: Deraniyagala, 1948, 1951, 1955; Patterson, in: Reilly et al., 1966; Bishop, 1967; Leakey, in: Bishop, 1967; Walsh and Dodson, 1969).

In March and April, 1948, a field party from the University of California African Expedition, led by H.B.S. Cooke, collected over 300 specimens of fossil mammals from deposits at Muruarot Hill. Until now, only one specimen, the skull of the rhinoceros Aceratherium acutirostratum (Deraniyagala), has been described from this large collection, almost all of which is presently conserved in the University of California Museum of Paleontology (UCMP), Berkeley. The new faunal components recorded in this paper, as well as those recorded by previous workers, support Arambourg's assignment of the Muruarot Hill fauna to the Early Miocene.

TABLE 1

FOSSIL MAMMALS PREVIOUSLY RECORDED FROM MURUAROT, WITH TAXONOMIC REVISIONS

ORIGINAL	REVISION
Hyaenodon andrewsi Savage[1]	
Kichechia zamanae Savage[1]	
Mastodon cf. *angustidens* Cuvier[2]	*Gomphotherium angustidens* (Cuvier)
Pliohyrax championi Arambourg[2]	*Megalohyrax championi* (Arambourg)[8]
Turkanatherium acutirostratum Deraniyagala[3]	*Aceratherium acutirostratum* (Deraniyagala)[9]
Aceratherium acutirostratum (Deraniyagala)[4]	*Aceratherium acutirostratum* (Deraniyagala) [in part] *Aceratherium* or *Dicerorhinus* sp. [in part]
Aceratherium? sp.[2]	*Aceratherium* or *Dicerorhinus* sp.
Listriodon jeanelli Arambourg[2]	*Bunolistriodon jeanelli* (Arambourg)[7]
Suidé indéterminé[2]	Suidae gen. et sp. indet.
Brachyodus? sp.[2]	*Brachyodus* sp. indet.
Dorcatherium chappuisi Arambourg[2]	
Dorcatherium pigotti Whitworth[5]	
Dorcatherium parvum Whitworth[5]	
Palaeomeryx africanus Whitworth[5]	*Propalaeoryx nyanzae* Whitworth[10]
Palaeotragus primaevus Churcher[6]	*Palaeotragus*? *primaevus* Churcher
Bovidé indéterminé[7]	Giraffoidea indet.
PECORA Incertae Sedis (medium and large spp.)[5]	PECORA indet. (medium and large spp.)

1. Savage (1965)
2. Arambourg (1933)
3. Deraniyagala (1951)
4. Hooijer (1968)
5. Whitworth (1958)
6. Churcher (1970)
7. Arambourg (1947)
8. Whitworth (1954)
9. Arambourg (1959)
10. Hamilton (1971, written communication)

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE

The University of California Museum of Paleontology faunal collection was recovered from two localities. The primary locality is designated Muruarot 2 (UCMP locality V-48100). Although Arambourg stated in his initial report (1933) and in subsequent ones (1943, 1947) that his fossils originated from Losodok, the members of the University of California field party found Arambourg's quarry at Muruarot 2 when they first began excavations in 1948 (Cooke, 1948, in manuscript; University of California African Expedition Field Catalogue; Phillips, 1949).

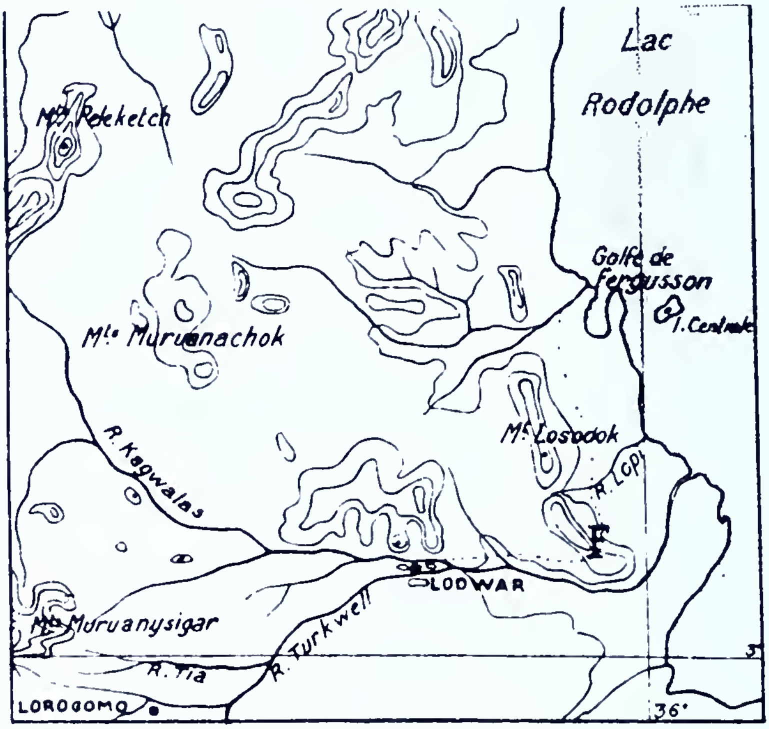

Figure 1. Map showing Muruarot Hill, which is just south of the Lopi River (R. Lopi). The site of Arambourg's fossil quarry is indicated by an "F". Adapted from Arambourg (1933).

This site also has yielded most of the fauna recorded by workers subsequent to Arambourg. It is located on the southeast slope of Muruarot Hill, approximately 20 miles N.E. of Lodwar and 12 miles W. of Lake Rudolf, in the Lothidok Hills region of northern Turkana District, northwestern Kenya (03° 15'N, 35° 47'E). The base of the principal fossiliferous stratum is about 1700 feet above sea level, some 90 feet above the present level of Lake Rudolf. The secondary locality, Muruarot 1 (UCMP locality V-4898), is situated on the north face of Muruarot Hill about three-fifths of a mile from the main site. The principal and virtually only fossiliferous bed is the same as that of Muruarot

2. The Muruarot general locality has been known in the past by several names and/or spellings, namely Losodok (Arambourg, 1933, 1943, 1947), Moruaret Hill (Deraniyagala, 1951; Hooijer, 1968), Moruorot South (Savage, 1965), Moruorot Hill (Churcher, 1970), Muruaret Hill (Deraniyagala, 1948), Lodwar, Moruoret and Moruorot (Bishop, 1967). The name Muruarot is used here since this name appears on the most recent geological map of the northern Turkana area (in: Walsh and Dodson, 1969).

The stratigraphic succession at Muruarot Hill and in the neighboring region was mapped and studied in detail by Arambourg in 1933 (Arambourg, 1933, 1943), Cooke in 1948 (personal field notes), and by Walsh and Dodson in 1963 (Walsh and Dodson, 1969). The following account of the stratigraphy is based upon the studies of these workers.

The Muruarot succession consists of approximately 640 feet of interbedded analcimic and augitic basalts and volcaniclastic sediments. The beds strike approximately north, dip from 15° to 23° west, and are well exposed on the north and southeast slopes of the hill. The principal fossiliferous level, which Cooke designated Bed 14, is the same as Arambourg's Bed 5 (Univ. Cal. Afr. Exped. Field Cat.), which yielded most of the fauna described by the latter worker (Arambourg, 1933, 1943). Cooke's Bed 14 consists of 8-15 feet of hard, fine grained, marly, purplish-red sandstones with conglomerate lenses. The upper surface of the bed is in many places cemented by plates of calcium carbonate; many of the fossils have been coated and impregnated with this mineral, thus insuring their preservation. Bed 14 is underlain and overlain by gray, flaggy sandstones, and it lies about 300 feet above the lowest observable beds. The Muruarot succession itself rests unconformably on a faulted basalt flow of unknown thickness and is overlain by a thick lava. The latter is in turn overlain by intercalated phonolites and purplish marls, which make up the summit of Muruarot Hill (Arambourg, 1933; Cooke, personal field notes). The analcimic and augitic basalts of the Muruarot succession belong to what the Geological Survey of Kenya calls the Tvb$_1$ Series (Walsh and Dodson, 1969). F.M. Consultants (in: Baker et al., 1971) have very recently dated whole rock samples from apparent Tvb$_1$ correlatives, the Samburu Basalts, near Maralal, Kenya, at 23 ± 3.2, 19.8 ± 3.1 and 18.5 ± 2.9 million years B.P. by K^{40}/A^{40}. These age determinations and correlations, if correct, suggest an Early Miocene age for the Muruarot basalts, interbedded sediments and fauna.

FAUNA

The fauna collected from Muruarot Hill includes fresh-water gastropods, fishes (*Polypterus*), trionychid turtles, crocodiles, pythonine snakes, and mammals ranging in size from small rodents to large proboscideans. As mentioned above, there are over 300 mammalian fossils in the University of California collection. All but about thirty of these specimens are identifiable to species, genus, family, or superfamily. The great majority of the identifiable fossils consist of either postcranial bones or jaws and teeth, a few of which show signs of having been gnawed by rodents. The original 1948 collection yielded only two skulls: a rodent, which probably represents Paraphiomys pigotti Andrews, and the previously mentioned rhinocerotid, Aceratherium acutirostratum (Deraniyagala). The latter is conserved in the Colombo National Museum, Ceylon. Only one skeleton, referable to a new palaeomerycid girrafoid genus and species soon to be described by Dr. W.R. Hamilton, is present in the collection. Eleven mammal skeletons have been reported previously from the Miocene of East Africa (Clark and Thomas, 1951; Mac Innes, 1956, 1957; Butler, 1956; Whitworth, 1958; Napier and Davies, 1959; Hooijer, 1966). The Muruarot skeleton will be described shortly by Dr. W.R. Hamilton of the Department of Paleontology, British Museum (Natural History). The dominant groups in the Muruarot fauna are long-limbed rhinoceroses and suiform and pecoran artiodactyls.

The mammalian faunal components in the University of California collection are listed in Table 2 along with those previously recorded from Muruarot Hill. The Muruarot fauna is similar to that collectively recorded from Rusinga Island, Lake Victoria, Kenya (see Bishop, 1967), and, indeed, it appears that there are few East African sites that have a fauna which is more like that of Rusinga Island than Muruarot. Most of the Rusinga fauna has been recovered from the Hiwegi Formation, which has been estimated to be about 18.5 million years old by its stratigraphic position in relation to other radiometrically dated strata (Van Couvering and Miller, 1969). This estimation provisionally places the Hiwegi Formation and its fauna within the later part of the Early Miocene.

Of special interest in the Muruarot fauna are the ape Dryopithecus nyanzae (Clark and Leakey) and two large giraffoids. The ape is represented by an infant mandibular ramus (UCMP 52112) which possesses a nearly complete deciduous fourth premolar; an erupting permanent first molar, an anterior portion of the second molar; a distal portion of the permanent canine; and the unerupted permanent third and fourth premolars. D. nyanzae has been recorded previously from Rusinga Island, Songhor, Koru and Maboko Island (Clark and Leakey, 1951; Pilbeam, 1969). The large giraffoids are the giraffid Palaeotragus primaevus Churcher and the palaeomerycid Palaeomeryx Meyer, which has only been recorded previously from Rusinga Island and Bukwa II, Uganda (Whitworth, 1958, Walker, 1969). The former species is almost certainly congeneric with a new taxon soon to be described by Hamilton (Madden; in preparation); the latter species, represented by a single very large, brachyodont upper molar (UCMP 41975), appears to be the largest palaeomerycid known from Early Miocene deposits. These giraffoids, as well as ones soon to be described by Hamilton (1971, written communication),

TABLE 2

LIST OF MAMMALIAN FAUNA FROM MURUAROT 1 AND 2

		1	2
PRIMATES			
Pongidae:	*Dryopithecus nyanzae* (Clark & Leakey)	X	-
RODENTIA			
Phiomyidae:	*Paraphiomys pigotti* Andrews	X	X
CREODONTA			
Hyaenodontidae:	*Anasinopa leakeyi* Savage	-	X
	Hyaenodon andrewsi Savage*	-	X
	gen. et sp. indet.	X	X
CARNIVORA			
Viverridae:	*Kichechia zamanae* Savage*	-	X
PROBOSCIDEA			
Gomphotheriidae:	*Gomphotherium angustidens* (Cuvier)*	-	X
	gen. et sp. indet.	X	X
Deinotheriidae:	*Prodeinotherium bavaricum* (Meyer)	X	X
HYRACOIDEA			
Procaviidae:	?*Prohyrax tertiarius* Stromer	-	X
Geniohyidae:	*Megalohyrax championi* (Arambourg)*	X	X
PERISSODACTYLA			
Rhinocerotidae:	*Aceratherium acutirostratum* (Deraniyagala)*	-	X
	Aceratherium or *Dicerorhinus* sp.*	X	X
	gen. et sp. indet.	X	X
ARTIODACTYLA			
Suidae:	*Palaeochoerus dartevellei* Hooijer	-	X
	Palaeochoerus sp. indet. [small sp.]	X	X
	Listriodon sp. indet. [small sp.]	-	X
	Bunolistriodon jeanelli (Arambourg)*	X	X
	Diamontohyus africanus Stromer	-	X
	gen. et sp. indet.*	X	X
Anthracotheriidae:	*Brachyodus* sp. indet.*	?	X
Tragulidae:	*Dorcatherium chappuisi* Arambourg*	-	X
	Dorcatherium pigotti Whitworth*	X	X
	Dorcatherium parvum Whitworth*	-	X
Palaeomerycidae:	*Propalaeoryx nyanzae* Whitworth*	X	X
	Palaeomeryx sp. indet. [large sp.]	-	X
	gen. et sp. nov.	X	X
Giraffidae:	*Palaeotragus*? *primaevus* Churcher*	X	X
Giraffoidea indet.:	[medium and large spp.]*	X	X
Bovidae:	*Walangania africanus* (Whitworth)	X	-
Pecora indet.:	[medium and large spp.]*	X	X

*Fossil mammals previously recorded from Muruarot Hill.

demonstrate that the Giraffoidea were a highly diversified group by the beginning of the Miocene Epoch and that their origin must date back to the Late Oligocene and perhaps even earlier.

AGE

Since 1948 there have been four or more hypotheses proposed as to the age of the Muruarot fauna (see Table 3). Deraniyagala (1948, 1951, 1955) felt that the fauna was either Pleistocene or Pliocene, but other workers such as Patterson (in: Reilly et al., 1966) and Walsh and Dodson (1969) have suggested a Late Miocene age. The hypotheses of these workers have been largely based upon two bovid horn cores which were apparently recovered from superficial deposits at Muruarot Hill. It is widely held that horned bovids do not appear in the geological record until Late Miocene times, and thus their presence in any fauna supposedly indicates that that particular fauna cannot be older than Late Miocene in age. Horned bovids, namely Gazella, Eotragus and Protragocerus, have now, however, been reported from the Early Miocene of Gebel Zelten, Libya by Hamilton (1971, written communication); and Hamilton also has transferred the East African Early Miocene pecoran Walangania africanus (Whitworth) to the Bovidae. Consequently, it can now be concluded that the Muruarot fauna could be older than the Late Miocene even if the horn cores belong to that fauna, which they probably do not.

The confusion about the age of the Muruarot fauna has resulted because two faunas of differing ages have been recovered from the locality. One of these faunas is of Tertiary age; the other is probably Quaternary. The latter consists of Equus, Phacochoerus, Alcelaphus and Connochaetes. This fauna yielded one of the bovid horn cores (Univ. Cal. Afr. Exped. Field Cat.) mentioned above, and perhaps the other. The Tertiary fauna is almost certainly of Early Miocene age. This is indicated because the fauna recorded here (Tables 1 and 2) is taxonomically similar to that collectively recorded from Rusinga Island. Thus, Arambourg (1933) was almost certainly correct in his assignment of the Muruarot Hill fauna to the Early Miocene.

ENVIRONMENT

The environment of Muruarot Hill at the time of the fauna's deposition appears to have been a semi-arid, relatively open one with shallow, swampy lakes. This reconstruction is based on preliminary analysis of the fossil-bearing sediments by Professor R. Hay, on analysis of the associated gastropod fauna by Mr. D. Van Damme and Dr. A. Gautier, and on the presence of certain mammalian species in the collection from the locality.

Hay (1971, personal communication) states that the matrix samples from the fossil-bearing level, Bed 14, are analcime-

no. 14

TABLE 3

PREVIOUS HYPOTHESES AS TO THE AGE OF THE MURUAROT FAUNA

WORKER	CONCLUSION
Arambourg (1933)	Early Miocene
Cooke (1948, in manuscript)	Early Miocene
Deraniyagala (1948)	Pleistocene
Deraniyagala (1951)	Pliocene
Deraniyagala (1955)	Pleistocene
Patterson (in: Reilly et al., 1966)	Late Miocene
Bishop (1967)	?Early Miocene
Leakey (in: Bishop, 1967)	Early Miocene and Late Miocene or Pliocene
Patterson (in: Walsh and Dodson, 1969)	Late Miocene
Walsh and Dodson (1969)	Late Miocene

bearing red sandstones similar to other analcimic red beds such as the Chinle (Triassic) of Utah and Wyoming and those of Olduvai Gorge in Tanzania. Such deposits are generally thought to be indicative of saline, alkaline chemical conditions in semi-arid or arid environments (Hay, 1966). Thus, minimally, a semi-arid environment seems to be indicated for the locality.

The gastropod fauna described from Muruarot by Van Damme and Gautier (1972) consists of Lanistes carinatus (Oliver), Pila ovata (Oliver), Cerastua miocenica (Vercourt) and Burtoa nilotica verdcourti Crowley and Pain. Van Damme and Gautier (1972) conclude that these gastropods, which were found in direct association with the Miocene mammal fauna, indicate a relatively open habitat with shallow, swampy lakes. Similar gastropods are also recorded from Muruarot by Verdcourt (1963), who also concludes that the paleoenvironment of the locality included swampy lakes.

The reconstruction given here for the Muruarot paleoenvironment is also based upon the presence of certain mammal species in the fauna. For example, Whitworth's study of the postcranial skeleton of the large hyracoid Megalohyrax championi (Arambourg), particularly the fore and hindlimbs, led him to conclude that this creature was almost certainly adapted for rapid locomotion in relatively open country, the most suitable habitats being either parkland or savannah. Similarly, the small proboscidean Prodeinotherium bavaricum (Meyer) and the large anthracothere Brachyodus Depéret are typical of lacustrine and riverine sites of Miocene age in East Africa (Bishop, 1968). The recovery of the above mammal species from the Muruarot localities partly reinforces the conclusions based upon the sediments and gastropods that the Muruarot environment was a semi-arid, rather open one with shallow, swampy lakes. The Muruarot paleoenvironment seems to have been strikingly similar to some of the habitats of Rusinga Island, which during Early Miocene times appears to have been principally an area of semi-arid habitats, namely parklands, steppes and savannahs with shallow, ephemeral lakes and flood plains (Whitworth, 1953, 1958). The presence of the ape Dryopithecus nyanzae at Muruarot indicates that it most probably inhabited the semi-arid, relatively open environment.

The Muruarot general locality has yielded one of the more complete and one of the oldest mammalian faunas known from East Africa. This fauna should become, when the Muruarot interbedded lavas are isotopically dated, one of the best dated of all African fossil mammal faunas. This report extends the paleozoogeographic range of the following mammals to Muruarot Hill: Dryopithecus nyanzae, Anasinopa leakeyi, Prodeinotherium bavaricum, Palaeochoerus dartevellei, Palaeochoerus, Listriodon, Diamontohyus africanus and Walangania africanus. Additional faunal components from Muruarot Hill are present in the Kenya National Museum in Nairobi. These specimens await description and taxonomic identification. The field party from the University of California African Expedition also collected a small sample of fossil mammals from nearby Lothidok (=Losodok) Hill. Since the fossils recorded from Lothidok by Arambourg (1933) are actually from Muruarot Hill, the mammals collected by the University of California party constitute the first fauna ever recovered from Lothidok Hill. This fauna has very recently been the subject of a brief study (see: Madden, 1972, in manuscript).

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THE HEMINGFORDIAN MAMMAL FAUNA OF THE VEDDER LOCALITY, BRANCH CANYON FORMATION, SANTA BARBARA COUNTY, CALIFORNIA. PART I: INSECTIVORA, CHIROPTERA, LAGOMORPHA, AND RODENTIA (SCIURIDAE).

by

J. Howard Hutchison and Everett H. Lindsay

THE HEMINGFORDIAN MAMMAL FAUNA OF THE VEDDER LOCALITY, BRANCH CANYON FORMATION, SANTA BARBARA COUNTY, CALIFORNIA

PART I: INSECTIVORA, CHIROPTERA, LAGOMORPHA, AND RODENTIA (SCIURIDAE)

BY J. HOWARD HUTCHISON[1]

AND EVERETT H. LINDSAY[2]

ABSTRACT

The Vedder mammal locality of Hemingfordian Land Mammal Age is located in a non-marine tongue of the predominantly marine Branch Canyon Formation. The Branch Canyon Formation has "Temblor" Stage megainvertebrate fossils and Saucesian Stage foraminiferal fossils. Taxa from the locality include a shrew (cf. *Limnoecus* sp.), mole (*Scalopoides* sp.), bat (?Phyllostomatidae), rabbit (*Hypolagus* cf. *H. apachensis*), pika (*Cuyamalagus dawsoni* n. gen., n. sp.), ground squirrel (*Miospermophilus* sp.), and flying squirrel (*Blackia* sp.). Rodents and horses to be discussed in subsequent parts of the faunal study form the basis for the age determination of the fauna.

INTRODUCTION

Hemingfordian mammal faunas are rare in the Pacific Coast region of North America. Most of those previously described are large-mammal assemblages. The Vedder locality provides the most diverse small-mammal Hemingfordian fauna yet known from this large area. Description of the fauna is divided into three parts; this part includes the Insectivora, Chiroptera, Lagomorpha, and sciurid Rodentia. Part II will include the eomyid and heteromyid Rodentia; Part III will include the larger mammals.

Fossils described below were collected from a single locality discovered by J. G. Vedder in 1967 while mapping the marine Branch Canyon Formation west of the Cuyama Badlands. Most of the fossil vertebrates previously collected in Cuyama Valley were found in sediments of the Caliente Formation on the east and north sides of Cuyama Valley in parts of Ventura and Santa Barbara counties, California. Fossil mammals from the Cuyama Badlands were first reported by C. L. Gazin (1930). Later reports on the fossil fauna were made by A. E. Wood (1937), V. L.

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VanderHoof (1939), J. F. Dougherty (1940), C. Stock (1947), D. E. Savage (1957), and C. A. Repenning and J. G. Vedder (1961). G. T. James (1963) published a comprehensive study of the Cuyama Badlands fossil vertebrate fauna based on extensive reconnaissance and collecting, including underwater screen washing, of previously known and new localities. As noted by earlier authors and summarized by James, the Caliente Formation of Cuyama Valley contains a diverse and long-ranging fauna. James recognized mammal faunas assignable to four North American Land Mammal Ages (Hemingfordian, Barstovian, Clarendonian, and Hemphillian) in the Caliente Formation.

The Vedder locality is west of the Cuyama River in a tributary of Tennison Canyon, 34° 51' 05" N, 119° 33' 13" W, at an elevation of 3120 feet, Santa Barbara County, California. The beds containing the site are tilted and locally faulted. Fossils were recovered from a mottled, brown and green mudstone overlying a localized six-inch-thick white limestone and underlying oyster-bearing beds. The present sample from the site includes only mammals. Collections from this locality are preserved in the University of California Museum of Paleontology and United States Geological Survey at Menlo Park where they are catalogued under locality numbers V6761 and M-1090 respectively. The latter collection consists of only larger vertebrates and the initial discovery material. Small vertebrates were recovered by underwater screening of about 750 to 1000 pounds of matrix collected by University parties. One millimeter pore brass screen (24 mesh) was used.

The Branch Canyon Formation is a lateral equivalent of the lower part of the Caliente Formation (Repenning and Vedder, 1961). Vedder (in letter, 1972) states, "the red bed zone from which the vertebrate material was collected contains marine invertebrate assemblages of middle Miocene age ("Temblor" Stage) west of M-1090 so that there is no apparent correlation problem...More than 1,500 feet of strata beneath the vertebrate locality contain middle Miocene mollusks, and the only Saucesian forams from the marine sequence north of Fox Mountain were collected about 1,400 feet below it."

The Hemingfordian age of the Vedder local fauna is based primarily upon specific identity of several rodents with those at Hemingfordian sites in the Great Plains (especially Martin Canyon Quarry A of Wilson, 1960; see McKenna, 1965:17, regarding the mammal age assignment of Quarry A) and identity of the equids with those at other Californian localities generally considered Hemingfordian in age.

Taxonomic parts of this paper were compiled separately by Lindsay (rodents) and Hutchison (other mammals). Augusta F. Lucas, staff artist of the Museum of Paleontology, drew figures 5 and 7. The authors drew the remaining figures. Terminology and abbreviations for dental characters of the Sciuridae are illustrated in figure 6. Terminology for other groups follows that in general usage. All measurements are given in millimeters. Abbreviation UCMP refers to University of California Museum of Paleontology.

SYSTEMATICS

Order INSECTIVORA Illiger, 1811

by J. H. Hutchison

Family TALPIDAE Fischer von Waldheim, 1817

Subfamily TALPINAE Fischer von Waldheim, 1817

Tribe SCALOPINI Trouessart, 1879

Genus _Scalopoides_ Wilson, 1960

Stratigraphic and geographic occurrence: Pawnee Creek Formation, Logan County, Colorado; Colter Formation, Teton County, Wyoming; Monroe Creek Formation, Shannon County, South Dakota; Deer Butte Formation, Butte Creek Volcanic Sandstone, and Juntura Formation, Malheur County, Oregon; Beatty Butte, Harney County, Oregon; Guano Ranch, Lake County, Oregon; Branch Canyon Formation, Santa Barbara County, California.

Age: Arikareean, Hemingfordian, Barstovian and Clarendonian.

Scalopoides sp.

Material: UCMP loc. V6761 - UCMP 96281, damaged left M^1; UCMP 96282, damaged right humerus lacking distal end, head, and parts of tuberosities and pectoral crest; UCMP 96283, left metacarpal V; UCMP 96284, damaged metacarpal IV; UCMP 96285-96286, two proximal phalanges of manus; UCMP 96287, unciform; UCMP 96388, damaged ungual phalanx of manus.

Description: A damaged M^1 (Fig. 1a) resembles the Barstovian _Scalopoides_ _ripafodiator_ Hutchison (1968) from Oregon in proportions and relatively small metaconule. M^1 of _S._ _isodens_ Wilson (1960) from the Hemingfordian Martin Canyon Quarry A, Colorado, is not known.

The humerus (Fig. 1b) resembles _Scalopoides_ in major features and _S._ _ripafodiator_ more closely than _S._ _isodens_. It is slightly smaller and proportionately more slender and delicate than that of _S._ _ripafodiator_.

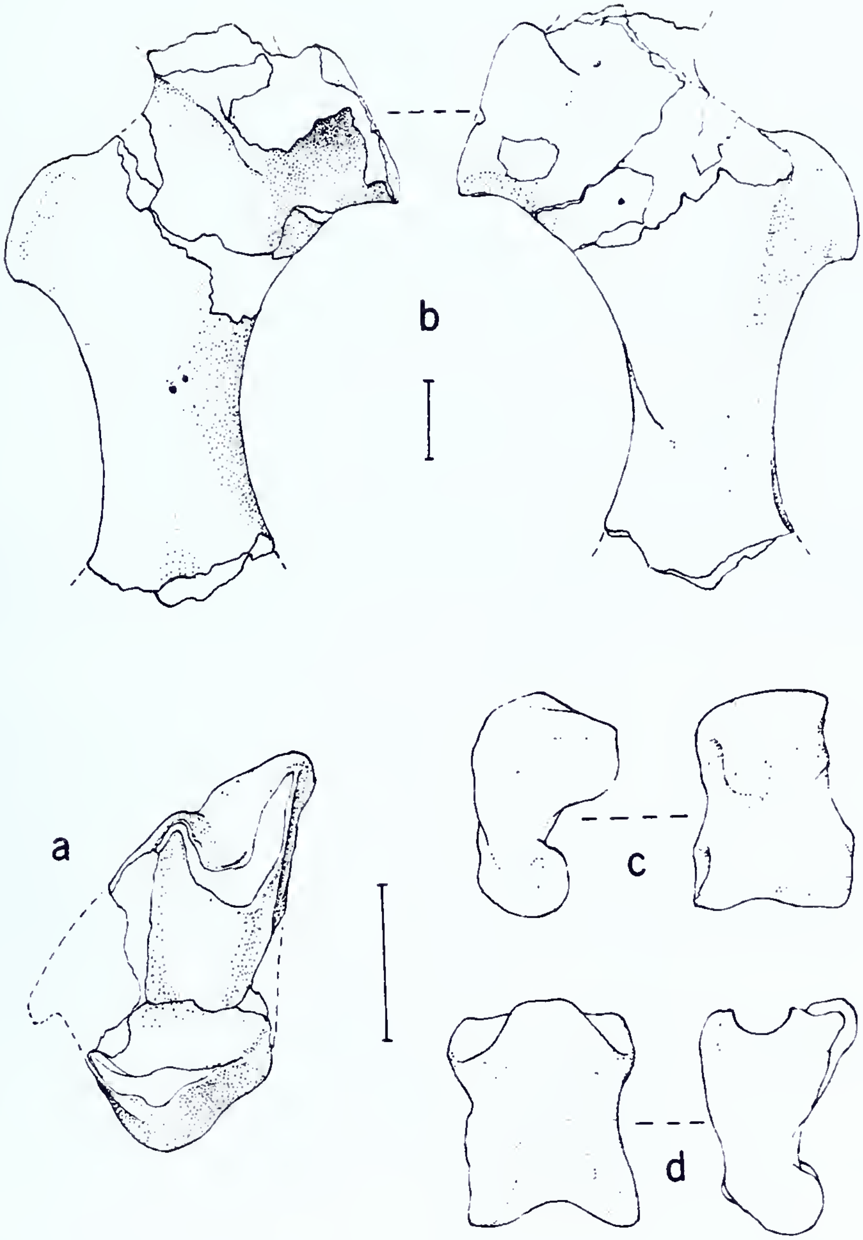

Fig. 1. *Scalopoides* sp. a. UCMP 96281, damaged left M^1, occlusal view. b. UCMP 96282, damaged left humerus, anterior (right) and posterior views. c. UCMP 96283, left metacarpal V, lateral and ventral views. d. UCMP 96285, proximal digit of manus, dorsal and lateral views. Scale lines = 1 mm.

Metacarpal V (Fig. 1c) and metacarpal IV are not directly comparable to the named species of Scalopoides. In comparison with metacarpal III of S. ripafodiator (Hutchison, 1968, fig. 58), the Vedder specimens are perhaps more slender, but are not as long as in Neurotrichus gibbsii (Baird). Two proximal phalanges of the manus (Fig. 1d), probably from digits II, III or IV, are about as squat as in S. isodens and thus shorter than some post-Barstovian specimens referred to Scalopoides (Hutchison, 1968;78, Table 17). UCMP 96287 is the first unciform assignable to Scalopoides but at present sheds little light on the relationships of this species.

Discussion: General agreement in size, functional grade, and comparative morphology of the Vedder talpid specimens indicates they represent only one species. The overall slenderness of elements indicates a mole less specialized postcranially than the Barstovian Scalopoides ripafodiator from Oregon, which in turn is less specialized than the early Hemingfordian S. isodens from Colorado. Robustness of the proximal phalanges is probably not significant considering the wide range in proportions in the small samples available for comparison and lack of knowledge of which digit they represent. The Vedder Scalopoides as presently known would provide a temporally suitable ancestor for S. ripafodiator but not for S. isodens. It indicates the presence of at least two lineages of Scalopoides in the Hemingfordian.

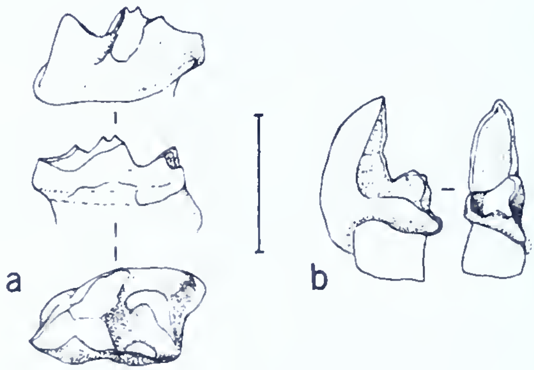

Fig. 2. Cf. Limnoecus sp. a. UCMP 82147, right M_1, labial, lingual, and occlusal views. b. UCMP 82145, left I^1, lingual and posterior views. Scale line = 1 mm.

Family SORICIDAE Fischer von Waldheim, 1817

Subfamily LIMNOECINAE Repenning, 1967

Genus Limnoecus Stirton, 1930

Stratigraphic and geographic occurrence: Pawnee Creek Formation, Logan County, Colorado; Split Rock Formation, Fremont County, Wyoming; Valentine Formation, Cerry County, Nebraska; Ogallala Formation, Trego County, Kansas; Butte Creek Volcanic Sandstone and Rome beds, Malheur County, Oregon; Barstow Formation, San Bernardino County, California; Caliente Formation, Ventura County, California; Branch Canyon Formation, Santa Barbara County, California.

Age: Hemingfordian, Barstovian, Clarendonian, and Hemphillian.

Cf. Limnoecus sp.

Material: UCMP loc. V6761 - UCMP 82145, heavily worn left I^1; UCMP 82147, nearly complete but damaged and heavily worn right M_1; UCMP 82146, left dentary fragment with broken M_1; UCMP 96078, 96080, broken tips of two lower anteromost incisors; UCMP 96079, M_1 fragment.

Description: A single relatively complete M_1 (Fig. 2a) is damaged and heavily worn but compares favorably with the M_1 of Limnoecus tricuspis Stirton in preserved details and size. The reentrant valley between protoconid and hypoconid emerges labially well above the cingulum. Anterior and labial cingula are well developed as in Limnoecus, unlike Antesorex Repenning. The dentary fragment includes the mental foramen below and anterior to the tip of the M_1 protoconid as in Limnoecus, Angustidens Repenning, and Antesorex.

I^1 (Fig. 2b) has a nonbifid principal cusp, narrow basilabial cingulum, and bicuspid (?) heel with labial cusp predominating in wear. The unworn heel may have had a single, transversely elongate cusp, but if so, wear tended to bifurcate this cusp.

Fragments of two lower incisors show that at least one prominent cusp lies posterior to the tip.

Discussion: In combination, position of the mental foramen, structure and delicacy of I^1 and M_1, and small size exclude the Vedder shrew from all Miocene genera except Limnoecus (see Repenning, 1967). Although in agreement with Limnoecus in the above characters, poor preservation and lack of more diagnostic parts preclude definite assignment of the Vedder shrew to Limnoecus. Only one species seems indicated in the sample.

Order CHIROPTERA Blumenbach, 1779

by J. H. Hutchison

Suborder MICROCHIROPTERA Dobson, 1875

Family PHYLLOSTOMATIDAE Coues and Yarrow, 1875

Stratigraphic and geographic occurrence: Honda Formation, Colombia; Caliente Formation, Ventura County, California; ?Branch Canyon Formation, Santa Barbara County, California; Pleistocene and Recent of North and South America.

Age: Hemingfordian to Recent in North America.

?Phyllostomatidae *incertae sedis*

Material: UCMP loc. V6761 - UCMP 82144, left lower canine; UCMP 80324, edentulous and incomplete right dentary.

Description: Canine crown (Fig. 3a) consists of a single hemiconical cusp, flattened posteriorly, and centered over the anterior moiety of the root. Labial and lingual cingula rise anteriorly. Two small cuspids, central and lingual, surmount the posterior cingulum; the posterolabial corner of the cingulum is either excavated or removed by shear. The root is robust, straight, and ovate to circular in cross-section.

The dentary (Fig. 3b) consists of two fragments found together in the same sieving screen and assumed to belong to one individual, although no contact is preserved. Fragments of roots are preserved in several alveoli. The anterior segment is bounded by breaks at the level of the canine and M_2. Four alveoli between M_1 and canine alveoli are interpreted to have held a double-rooted P_4 and either a single-rooted P_2 and reduced single-rooted P_3 or a double-rooted P_2 or P_3; the former condition seems more likely considering the lack of alveolar coalescence and typical phyllostomatid anterior root reduction during antemolar shortening. Dental homologies will thus be considered as I?, C1, P2, P3, P4, M1-M3 (following Miller, 1907). The dentary is curved both vertically and horizontally and has a large oblique symphyseal scar. A mental foramen exists below P_2 and a small foramen is present just posterior to the symphysis.

Discussion: Dentary and canine may represent more than one taxon; however, the two specimens indicate comparable-sized individuals and will be treated as one species.

Among Microchiroptera available for comparison in the University of California Museum of Vertebrate Zoology at Berkeley, members of the Phyllostomatidae most closely approach the charac-

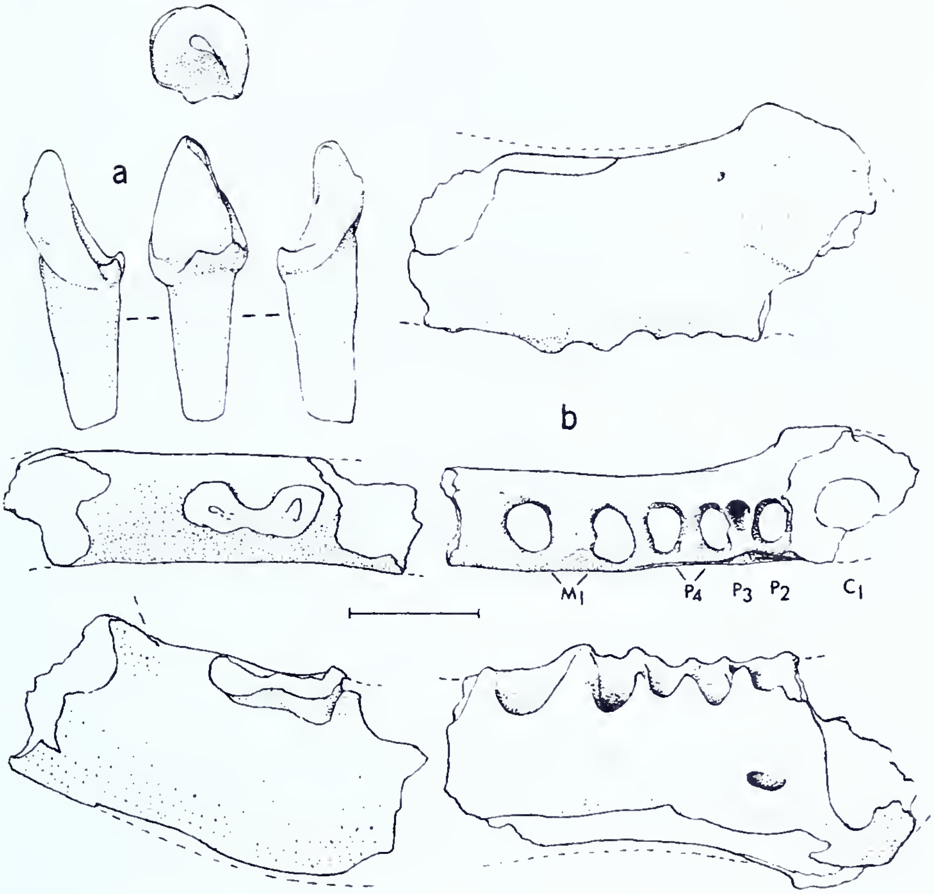

Fig. 3. ?Phyllostomatidae incertae sedis. a. UCMP 82144, left lower canine, labial, posterior, lingual, and occlusal views. b. UCMP 80324, right dentary fragments, lingual, dorsal, and labial views. Scale line = 1 mm.

ters of the fossils. Of the recent genera resembling the fossils (Chilonycteris Gray, Pteronotus Gray, Lonchorhina Tomes, Macrophyllum Gray), no genus is identical to the fossil material, but Macrophyllum macrophyllum (Wied) is similar in general shape of the dentary, position and expanse of symphyseal scar, dental formula, and alveolar positions. In contrast to the fossils, the canine of M. macrophyllum is longer than wide in occlusal dimensions and possesses only one cusp on the posterior cingulum.

While the Vedder bat certainly represents a new species, the fragmentary nature of these specimens and possibility of future work at the site advise deferring assignment of a new name.

Order LAGOMORPHA Brandt, 1855

by J. H. Hutchison

Family LEPORIDAE Gray, 1821

Genus Hypolagus Dice, 1917

Hypolagus apachensis Gazin, 1930

Stratigraphic and geographic occurrence: Known only from California - Caliente Formation, Ventura County; Mint Canyon Formation, Los Angeles County; ?Branch Canyon Formation, Santa Barbara County.

Age: Hemingfordian, Barstovian, and Clarendonian.

Hypolagus cf. H. apachensis

Material: UCMP loc. V6761 - UCMP 82482, fragment of right dentary with damaged P_3-P_4.

Description: Labial side of dentary (Fig. 4a) below and anterior to P_3 is fenestrated. Lingually the lower incisor root terminates above the level of fenestration and extends posterad to the anterior moiety of P3 P3 (Fig. 4b, c) is elongate (this is exaggerated due to oblique breakage of the crown). Deep cement-filled labial and lingual hypostriae separate talonid from trigonid and persist to base of exposed crown. A broad shallow anterolabial hypostria appears to lack cement although this may have been lost after death.

Discussion: Fragmentary nature of the Vedder leporid prevents definitive taxonomic assignment. Combination of elongate P_3 and shallow anterolabial hypostria are characteristic of Dawson's (1958:38) Archaeolagus group (A. ennisianus (Cope) and A. macrocephalus (Matthew), but a similar degree of development is also seen in some species of Hypolagus. Persistent internal hypostria on P_3 is present in some specimens of H. apachensis (e.g., Fig. 25c and discussion, p. 17, of Dawson, 1958). Dawson (1958:63) considered high posterior termination of the lower incisor as typical of Hypolagus, and, in combination with tooth morphology assignment of the Vedder leporid to Hypolagus is more reasonable. The Vedder Hypolagus, as known, is in suitable chronologic and geographic position for ancestry to other known H. apachensis, to which it is tentatively referred.

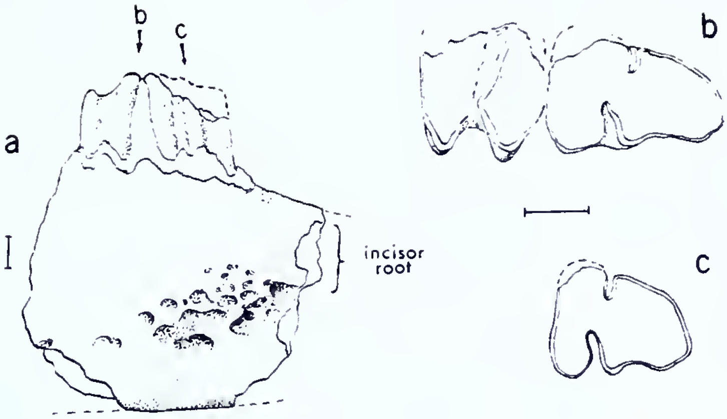

Fig. 4. Hypolagus cf. H. apachensis, UCMP 82482, right dentary fragment with P_3-P_4. a. Labial view with arrows indicating angle of occlusal views. b. Occlusal view of P_3-P_4. c. Occlusal view of P_3 perpendicular to long axis of tooth. Scale lines = 1 mm.

Family OCHOTONIDAE Thomas, 1897

Cuyamalagus dawsoni Hutchison, n. gen., n. sp.[1]

Holotype: UCMP 82151, three lower right molariform teeth.

Hypodigm: Type and UCMP 82149, 82150, 80327, three incomplete upper molariform teeth.

Type locality and age: UCMP locality V6761, Vedder locality, Branch Canyon Formation, Santa Barbara County, California. Hemingfordian. Known only from type locality.

Diagnosis: Cheek teeth hypsodont but rooted. Upper molariform teeth with concave labial and convex lingual walls indicating unilateral hypsodonty, distinct crescentic valleys present, hypostriae cross about one third or less of occlusal width in early wear but fade out before reaching lingual base of crowns, anterolophs wider than posterolophs. Lower molars with talonids and trigonids separate to near base of crowns, talonids nearly as transversely broad as trigonids, posterior wall of trigonids slightly protruded, talonids with central anterior protrusion, posterolophids persistent 20% to 40% of depth, talonids becoming equal in length to trigonids with loss of posterolophids during wear.

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[1] From Cuyama - Cuyama Valley plus Greek lagos, hare. Specific name after Mary R. Dawson in recognition of her work on fossil lagomorphs.

Description: Molariform upper teeth show marked transverse curvature (Fig. 5a, b). UCMP 80327 shows two small labial roots and one massive lingual root. All specimens have anteroloph wider than posteroloph, distinct hypostriae, and crescentic valleys. Transverse depth of lingual hypostriae varies from fairly deep and close to crescentic valley in little-worn condition (Fig. 5a) to shallow (Fig. 5b, c) in more worn specimens. Crescentic valleys and hypostriae are cement-filled. The arrow in Figure 5b indicates terminus of the hypostria.

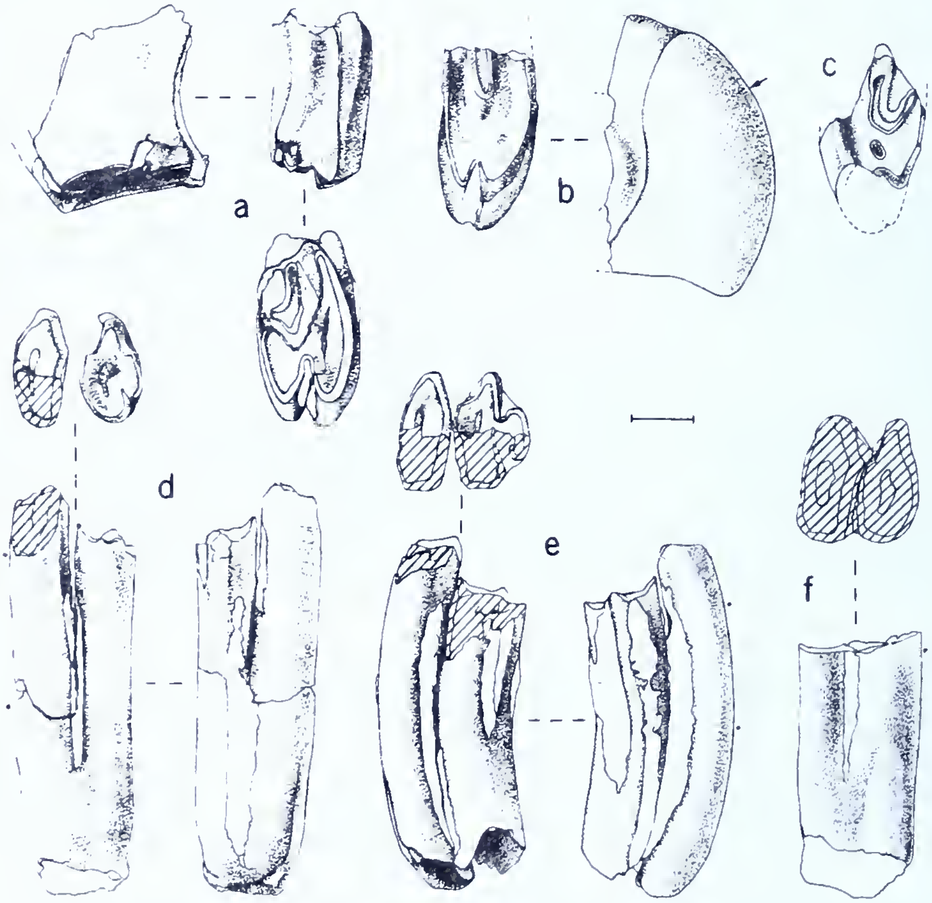

Fig. 5. Cuyamalagus dawsoni Hutchison, n. gen., n. sp. a. UCMP 82149, right upper molariform tooth (M^2?), occlusal, lingual, and posterior views. b. UCMP 80327, right upper molariform tooth, occlusal and anterior views. c. UCMP 82150, left upper molariform tooth fragment, occlusal view. d-f. UCMP 82151, holotype. d. Right P_4 or M_1, occlusal, lingual, and labial views. e. Right M_2, occlusal, lingual and labial views. f. Lower portion of right P_4 or M_1, occlusal cross-section and lingual view. The small dots along the side of the lower teeth represent levels at which measurements were taken. Scale line = 1 mm.

Three lower right molariform teeth appear to represent a single individual and unlike the upper teeth, were previously catalogued under a single number (probably indicating a single sieving screen or bag sample) and thus chosen for the type specimen. Two specimens (Fig. 5d, e) are complete enough to preserve their total heights. Both appear to be in early wear with hypoconulids still present and roots (in third specimen also) incomplete but closing. Trigonids and talonids on all lower teeth are separate to about the basal third of the tooth (75% to 90% of tooth height) but are amply joined by cement (mostly chipped away by breakage). Folds setting off hypoconulids from talonids are also cement-filled. Trigonids and talonids are subequal in width but talonids are longer in early wear, tending to become nearly equal to trigonids after loss of hypoconulids (posterolophids) with wear (Table 1). Labial margins of trigonids and talonids are persistently more angular than the lingual margins. Anterior protrusion of the talonid is well developed in early wear stages. A small protrusion labial to the center of the posterior wall of the trigonid is indicated in all three teeth. Indications of enamel thinning or loss are discernible on the labial sides of two specimens (Fig. 5d, f). Strong curvature and lesser root development on one specimen (Fig. 5e) suggests that this tooth is an M_2.

Discussion: Of the twenty named genera of ochotonids, only six (*Amphilagus* Pomel, *Titanomys* von Meyer, *Desmatolagus* Matthew and Granger, *Hesperolagomys* Clark, Dawson and Wood, *Russellagus* Storer, and *Gripholagomys* Green) retain roots and well developed molar crescents, but all these also have distinctly narrower talonids than trigonids (a primitive feature in ochotonids). A wide talonid is characteristic of more advanced ochotonids with evergrowing teeth.

While it is possible to speculate on the phyletic position of Cuyamalagus, lack of anterior premolars and jaw material leave too much latitude for profitable comparisons. Of the North American genera (see Green, 1972), only ?*Desmatolagus* (Hemingfordian) and *Gripholagomys* (Arikareean and Hemingfordian) are early enough and structurally primitive enough to be possible ancestral forms or close relatives of ancestral forms of *Cuyamalagus*. *Hesperolagomys* (Barstovian and Clarendonian) and *Russellagus* (Barstovian) retain a primitively narrow talonid and are thus unlikely descendents of *Cuyamalagus*. *Oreolagus* McGrew occurs in the early Hemingfordian (Green, 1972) and later but is too advanced in hypsodonty for close relationship with *Cuyamalagus*. While relationships of all North American Miocene ochotonid genera are largely unknown, the known diversity of these genera (six) is rapidly approaching that of Eurasia (eight in Europe and two in Asia - see Green, 1972, and Dawson, 1967).

TABLE 1

Measurements of _Cuyamalagus dawsoni_, n. gen., n. sp.

Upper Molariform Teeth	UCMP 82149	UCMP 80327
Length	1.54	1.55
Width of anteroloph	2.57	- -
Width of posteroloph	2.20	- -

Lower Molariform Teeth - UCMP 82151 (Type)

	P_4 or M_1	M_2	P_4 or M_1*
Length trigonid (top)	0.99	0.94	- -
Length talonid (top)	1.04	1.32	- -
Length trigonid (middle)	1.10	1.13	1.04
Length talonid (middle)	0.96	1.17	1.03
Width trigonid (top)	1.95	1.93	- -
Width talonid (top)	1.77	1.90	- -
Width trigonid (middle)	2.13	2.10	2.18
Width talonid (middle)	1.72	1.84	2.16
Height (base of enamel on labial side to top of trigonid)	6.72	5.85	- -
Length of crown	2.17	2.33	2.05

*incomplete specimen

RODENTIA Bowdich, 1821

by E. H. Lindsay

Family SCIURIDAE Gray, 1821

Subfamily SCIURINAE Baird, 1857

Genus *Miospermophilus* Black, 1963

Stratigraphic and geographic occurrence: Pawnee Creek Formation, Logan County, Colorado; Split Rock Formation, Fremont County, Wyoming; Branch Canyon Formation, Santa Barbara County, and Barstow Formation, San Bernardino County, California.

Age: Hemingfordian and Barstovian.

Miospermophilus sp. indet.

Material: UCMP loc. V6761 - UCMP 80326, right dP^4; UCMP 82138, left M_3; UCMP 82139, right P_4; UCMP 82141, left M^1 or M^2; UCMP 82142, right P^4, and UCMP 82143, P^3.

Description: P^3 - A small, round, peglike premolar is assigned to this taxon. The premolar is about 0.3 mm wide.

dP^4 - UCMP 80326 (Fig. 7b) has the anterocone and part of the anterior cingulum removed by breakage. Paracone and metacone are subequal, smaller than the prominent protocone. Protoconule and metaconule are absent from the high, narrow protoloph and metaloph uniting paracone and metacone (respectively) with the anterior and posterior sides of the protocone. Posterior cingulum is high and narrow, connecting the basal metacone and posterior protocone. An incipient hypocone is marked by an expansion on the internal posterior cingulum. The anterior cingulum is low where it joins the anterior protocone. A small mesostyle is placed between and slightly lateral to the paracone and metacone; a low lophule joins the mesostyle and posterior basal paracone. The central basin is wide, slightly rugose, and open laterally posterior to the mesostyle. The posterior basin is narrow, bounded by the metaloph and posterior cingulum.

P^4 - A badly corroded cheek tooth is probably P^4. Its occlusal outline is elongate oval, width greater than length; the anterolabial margin of the tooth is removed by breakage. The protocone is the most prominent cusp; paracone and metacone are subequal. A small metaconule is present on the metaloph; a protoconule is absent. The protocone is directly lingual to the paracone, and these cusps are connected by the narrow protoloph. Metaloph connects metacone and metaconule, it terminates short of the protocone. Anterior and posterior cingula were apparently present, but are largely obliterated by corrosion. Parastyle

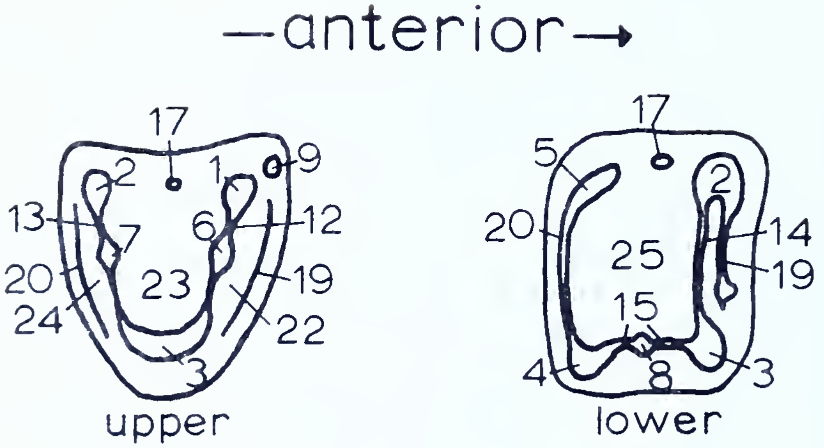

Fig. 6. Dental terminology for sciurid teeth. 1 - Paracone. 2 - Metacone (-id). 3 - Protocone (-id). 4 - Hypoconid. 5 - Entoconid. 6 - Protoconule. 7 - Metaconule. 8 - Mesoconid. 9 - Parastyle. 12 - Protolophule. 13 - Metalophule. 14 - Metalophid. 15 - Ectolophid. 17 - Mesostyle (-id). 19 - Anterior cingulum. 20 - Posterior cingulum. 22 - Anterior inner valley. 23 - Central valley. 24 - Posterior inner valley. 25 - Talonid basin.

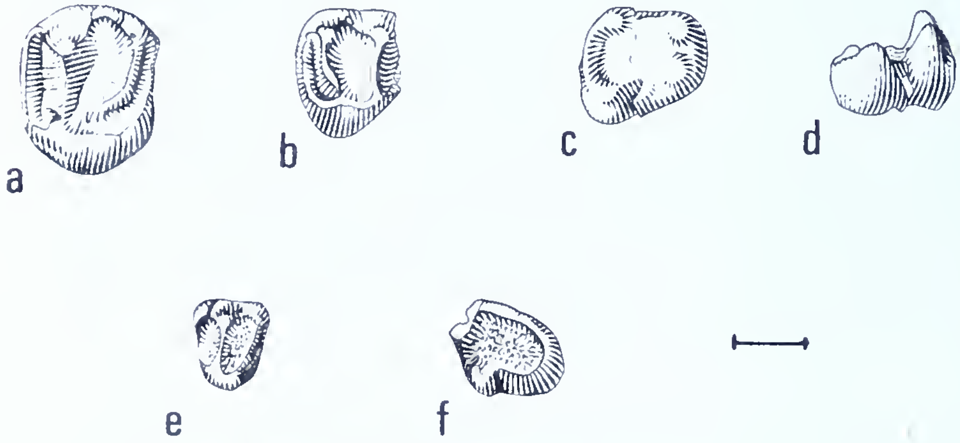

Fig. 7. Sciurid rodents. a-d. Miospermophilus sp. a. UCMP 82141, left M^1 or M^2, occlusal view. b. UCMP 80326, right dP^4, occlusal view. c. UCMP 82139, right P_4, occlusal view. d. UCMP 82139, right P_4, labial view. e-f. Blackia sp. e. UCMP 82140, left P^4, occlusal view. f. UCMP 82137, left M_3, occlusal view. Scale line = 1 mm.

and mesostyle were small or absent but breakage in that area prohibits a precise determination. The central basin is relatively narrow, but wider than anterior and posterior basins.

M^1 or M^2 - A well preserved and slightly worn tooth (Fig. 7a) is M^1 or M^2. Precise identification of this isolated tooth is impossible without associated teeth. Occlusal outline is subquadrate, width greater than length. Protocone, the most prominent cusp, is elongated anteroposteriorly. Metacone is lower and smaller than the paracone. An incipient hypocone is indicated by expansion of the lingual part of the posterior cingulum. A small metaconule is indicated by expansion of the metaloph; protoconule is absent. A minute parastyle is present on the labial margin of the anterior cingulum. A small mesostyle is present between and labial to the paracone and metacone. The protoloph is narrow, directed transversely, connecting paracone and anterior basal margin of the protocone. Metaloph is narrow, and connects the metacone and metaconule. A low and faint ridge continues lingual from the metaconule to the posterior base of the protocone. The anterior cingulum is narrow and relatively low, connecting the parastyle and anterior base of the protocone. Parastyle does not join the paracone. The posterior cingulum is low and narrow posterior to the metacone and high lingually where it joins the posterior side of the protocone. The central basin is relatively wide, slightly rugose, and closed by the mesostyle. The anterior basin is narrow, slightly rugose, and constricted labially. The posterior basin is very narrow, slightly rugose, and constricted both labially and lingually. A faint accessory loph is directed labially from the protocone.

P_4 - A slightly corroded but relatively unworn tooth (Fig. 7d) is identified as a P_4. Occlusal outline of this tooth is obovate, length greater than width; anterior width is less than posterior width. The posterolingual corner of the tooth is subangular. Metaconid and protoconid are prominent, with protoconid lower and placed slightly more posteriorly than the metaconid. Hypoconid is large; entoconid is small but distinct. Mesoconid is absent from the low and narrow ectolophid. Posterolophid is low and narrow, slightly arcuate between the hypoconid and entoconid. A low, rounded mesostylid is present on the lingual border between the metaconid and entoconid. Talonid basin is shallow and slightly rugose. Valley between the metaconid and protoconid is steep and narrow, with no indication of a loph connecting the cusps.

M3 - The posterior lower molar is represented by part of a broken tooth. Its occlusal outline is apparently an elongate oval with a rounded posterior margin. Metaconid is prominent and connected to the hypoconid by a high, continuous, wide, arcuate posterior cingulum. Talonid basin is shallow, slightly rugose, and closed posterolingually by the posterior cingulum. Measurements are given in Table 2.

TABLE 2

Measurements of sciurid rodents

Miospermophilus sp.		Length	Width
UCMP 82143	P^3	0.3	0.3
UCMP 80326	dP^4	- -	1.77
UCMP 82142	P^4	1.56	1.95
UCMP 82141	M^1 or M^2	1.95	2.34
UCMP 82139	P_4	1.88	1.62
UCMP 82138	M_3	(2.80)	- -
Blackia sp.			
UCMP 82140	P^4	1.04	1.25
UCMP 82137	M_3	(1.50)	(1.50)

Measurements in parentheses ( ) are approximate.

Discussion: The teeth of *Miospermophilus* sp. of the Vedder fauna are larger than those of *Miospermophilus bryanti* (Wilson) from Martin Canyon Quarry A, Logan County, Colorado, and *Miospermophilus* sp. from the Barstow Formation; they are about the size of *Miospermophilus wyomingensis* Black from the Split Rock Formation in Fremont County, Wyoming (Black, 1963). *Miospermophilus* of the Vedder fauna differs from *M. wyomingensis* in having a broader protocone, less prominent transverse lophs, and a more distinct entoconid. Observed differences between the Vedder *Miospermophilus* sp. and *M. wyomingensis* are slight.

Subfamily PETAURISTINAE Simpson, 1945

Genus *Blackia* Mein, 1970

Stratigraphic and geographic occurrence: Branch Canyon Formation, Santa Barbara County, California; Sansan, La Grive, and Soblay in France; Anwil, Switzerland; Wolfersheim, Germany.

Age: Hemingfordian, North America; middle Miocene to Pliocene, Europe.

Description: P^4 - A small, transversely elongate, relatively unworn tooth (Fig. 7e) is considered P^4. Its prominent protocone is high and narrow. Metacone is lower than the paracone and is placed slightly labial to it. A large parastyle is anterior and slightly lingual to the paracone. Protoconule, metaconule, hypocone, and mesostyle are absent. Protoloph and metaloph are narrow and high, joining anterior and posterior sides of the protocone. Anterior and posterior cingula are low, terminating lingually at the base of the protocone, terminating labially at the parastyle (anterior cingulum) and at the posterior side of the metacone (posterior cingulum). The central basin is distinctly rugose, wide, slightly cup-shaped, and closed labially by a low ridge (mesostylar ridge of Mein, 1970) connecting paracone and metacone. Anterior and posterior valleys are narrow, and open where cingula are very low. A distinct but small accessory loph is directed labially from the central area of the protocone.

M_3 - An isolated M_3 (Fig. 7f) is relatively unworn but its anterolingual corner is missing. The occlusal outline is elongate oval with its long axis directed obliquely. Protoconid is set off from the anterior cingulum and the ectolophid. Hypoconid is embedded in the high arcuate posterior cingulum near the rounded posterolingual corner. Incipient entoconid and mesostylid are indicated by slight swelling on the posterior cingulum along the labial border. Mesoconid and metalophid are absent. Talonid basin is wide, distinctly rugose, slightly cup-shaped, and closed except for the groove separating the posterior cingulum from posterior side of the protocone. Measurements are given in Table 2.

Discussion: These two isolated cheek teeth are referable to the Petauristinae because of their rugose occlusal surface, reduced anterior cingulum, and distinctive groove on M_3 between the anterior cingulum and protoconid. They are placed in the genus *Blackia* because of their small size, and simple molar structure (lacking the hypocone and conules in upper cheek teeth and lacking the mesoconid in lower cheek teeth). Two species of *Blackia* have been named. *Blackia miocaenica* is known from La Grive, Sansan, and Anwil in western Europe. *Blackia miocaenica* and *Blackia* sp. from the Branch Canyon Formation are smaller than *B. wolfersheimensis*. *B. miocaenica* was characterized by Mein (1970) as having a triangular P^4 with a high and narrow protocone and a strong parastyle. *Blackia* sp. of the Vedder fauna is very close to *B. miocaenica*, differing from that species in its slightly wider and more robust P^4. The North American record of *Blackia* probably represents a new species but specific assignment is withheld until more diagnostic characters can be defined.

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PALEOBIOS

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No. 16 April 30, 1974

THE HEMINGFORDIAN MAMMAL FAUNA OF THE VEDDER LOCALITY, BRANCH CANYON FORMATION, SANTA BARBARA COUNTY, CALIFORNIA.

PART II: RODENTIA (EOMYIDAE AND HETEROMYIDAE).

by

Everett H. Lindsay

no. 16

THE HEMINGFORDIAN MAMMAL FAUNA OF THE VEDDER LOCALITY, BRANCH CANYON FORMATION, SANTA BARBARA COUNTY, CALIFORNIA

PART II: RODENTIA (EOMYIDAE AND HETEROMYIDAE)

BY EVERETT H. LINDSAY[1]

ABSTRACT

The Vedder fauna is a Hemingfordian (middle Miocene) assemblage of land mammals from the dominantly marine Branch Canyon Formation in the Transverse Ranges of southern California. Five species of extinct rodents (_Eomys_ sp., _Pseudotheridomys cuyamensis_ n. sp., _Mookomys_ cf. _M. altifluminus_, _Proheteromys sulculus_, and _Proheteromys magnus_) from the Vedder locality, UCMP locality V6761, are described.

INTRODUCTION

The Vedder fauna was collected from the Branch Canyon Formation in a tributary of Santa Barbara Canyon on the west side of the Cuyama Valley. The Vedder locality, UCMP V6761, has produced a moderately large sample of small mammals and two small horses. Insectivora, Chiroptera, Lagomorpha, and sciurid rodents were described in The Vedder Fauna, Part I, by Hutchison and Lindsay (1974). Part II includes the description of two eomyid and three heteromyid rodents. Part III will include the description of a carnivore, a merychippine horse, an archaeohippine horse, and summary of the fauna. Age of the Vedder fauna is Hemingfordian Land Mammal Age (middle Miocene).

Abbreviations used in the text are: AMNH = American Museum of Natural History; FSGS = Florida State Geological Survey; UCMP = University of California Museum of Paleontology; UK = University of Kansas Museum of Natural History.

Abbreviations used in the table of measurements are: M = molar tooth; P = premolar tooth; N = number of specimens measured; $\bar{X}$ = mean of sample; S = standard deviation of sample; V = coefficient of variability; OR = observed range of measurements.

Terminology used for rodent teeth is illustrated in Figure 1.

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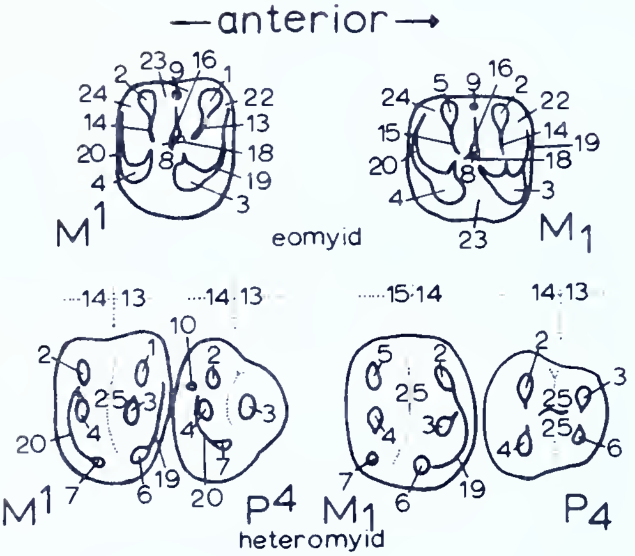

Fig. 1. Dental terminology for rodent teeth. 1 - Paracone. 2 - Metacone (-id). 3 - Protocone (-id). 4 - Hypocone (-id). 5 - Entoconid. 6 - Protostyle (-id). 7 - Hypostyle (-id). 8 - Mesocone (-id). 9 - Mesostyle (-id). 10 - Posterocone. 13 - Protoloph (-id). 14 - Metaloph (-id). 15 - Hypoloph (-id). 16 - Mesoloph (-id). 18 - Mure or ectoloph (-id). 19 - Anterior cingulum. 20 - Posterior cingulum. 22 - Anterior valley (lake). 23 - Outer valley. 24 - Posterior valley (lake). 25 - Transverse valley.

SYSTEMATICS

Order RODENTIA Bowdich, 1821

Family EOMYIDAE Depéret and Douxami, 1902

Genus *Eomys* Schlosser, 1884

Omegodus Pomel, 1853, Catalogue methodique..., p. 37.
Eomys Schlosser, 1884, Palaeontographica, 31: 84.

Eomys zitteli Schlosser, 1884

Stratigraphic and geographic occurrence: Branch Canyon Formation, Santa Barbara County, California; Burgmagerbein, Treuchtlingen, Gaimersheim, Bissingen, and Wintershof-West in western Europe.

Age: Hemingfordian of North America; Chattian, Aquitanian, and Burdigalian of Europe.

Eomys aff. *E. zitteli*

Material: UCMP loc. V6761 - UCMP 82148, right M$_2$.

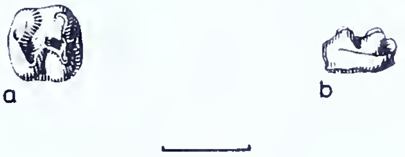

Fig. 2. *Eomys* sp., a, UCMP 82148, right M$_2$, occlusal view; b, UCMP 82148, right M$_2$, labial view; scale line equals 1 mm.

Description: UCMP 82148 is a slightly worn right M$_2$ with subquadrate occlusal outline. The anterior half of the tooth is slightly wider than the posterior. Four prominent cusps (metaconid, entoconid, protoconid, and hypoconid) are connected by metalophid, hypolophid, and central mure. Protoconid is compressed anteroposteriorly in comparison with the hypoconid. An anterior cingulum joins metalophid and anterior arm of the protoconid near the midline of the tooth. The anterior cingulum is moderately high lingually where it terminates anterior to the metaconid; the labial half of the anterior cingulum is short, terminating before reaching the anterolabial corner of the tooth. Posterior cingulum is short, directed lingually from the junction of the hypolophid and the posterior arm of the hypoconid. Posterior cingulum terminates before reaching the entoconid. Mesolophid is moderately high but short. A mesostylid and mesoconid are absent. Anterior and posterior inner valleys are narrow, and constricted (but open) lingually. Outer valley is relatively wide. Medial valley is steep-walled and deep but is open laterally. Crown height is low. Roots are not preserved. Measurements of UCMP 82148 are: length, 0.82 mm; width, 0.83 mm.

Discussion: The *Eomys* M$_2$ from the Vedder fauna is closest in size and morphology to *Eomys zitteli*, recorded from Chattian (late Oligocene) faunas of Europe, *i.e.*, Burgmagerbein and Treuchtlingen. It differs from that species primarily in smaller size (cheek teeth 45% smaller than the neotype of *E. zitteli*). Fahlbusch

(1968, 1970) has ably analyzed morphological variation in middle Tertiary eomyids, recognizing three species of Eomys (E. zitteli Schlosser, E. major Freudenberg, and E. rhodanicus Hugueney and Mein) in Europe. He characterized Eomys as a small brachydont rodent with four cheek teeth, each bearing four principal cusps connected by two transverse lophs and a mure. Similar genera are Rhodanomys Depéret, Apeomys Fahlbusch, Pseudotheridomys Schlosser, and Ligerimys Stehlin and Schaub. Eomys is directly ancestral to Rhodanomys, Pseudotheridomys, and Apeomys, differing from those genera in having lower crowned cheek teeth with weaker development of transverse lophs, greater prominence of cusps, and better development of the mure.

Probably Adjidaumo Hay, common in early and middle Oligocene deposits of North America, gave rise to European species of Eomys during the middle or late Oligocene. Cheek teeth of Eomys differ from those of Adjidaumo (Oligocene species) in better development of the mure and the anterior cingulum. Cheek teeth of Eomys differ from those of Pseudadjidaumo Lindsay (Miocene species) in weaker development of the anterior and posterior cingulum. Cheek teeth of Pseudadjidaumo are slightly higher crowned than Eomys, and usually have a mesostyle and mesostylid. Apparently eomyids were absent from North America during late Oligocene and early Miocene. In middle Miocene (Hemingfordian) Eomys and Pseudotheridomys invaded North America from Palearctica. Eomys of the Hemingfordian Vedder fauna is probably ancestral to Barstovian species of Pseudadjidaumo.

Genus Pseudotheridomys Schlosser, 1884

Pseudotheridomys cuyamensis n. sp.

Type: UCMP 80311, right P_4 from the Vedder locality, UCMP V6761.

Hypodigm: Type and 61 isolated cheek teeth (11 P^4, 15 M^{1-2}, 5 M^3, 10 P_4, 7 M_1, 5 M_2, and 8 M_3).

Type locality and age: UCMP locality V6761, Vedder locality, Branch Canyon Formation, Santa Barbara County, California. Hemingfordian. Known only from type locality.

Diagnosis: Anterior and posterior valleys of molars and premolars closed by high anterior and posterior cingula; mesoloph high and long on upper cheek teeth, usually contacting protoloph in early wear. Mesolophid high and long on lower cheek teeth, usually separate from the hypolophid until late wear.

Comparisons: Pseudotheridomys cuyamensis is larger than other known species of Pseudotheridomys. P. pagei Shotwell is slightly smaller than P. cuyamensis and has a more distinct lophid (ectolophid) connecting mesolophid and hypolophid in lower cheek teeth. P. hesperus Wilson has lower anterior and posterior cingula on its cheek teeth. *P. parvulus* (Schlosser), *P. pusillus* Fahlbusch, and *P. schaubi* Lavocat are all smaller than *P. cuyamensis* and their cheek teeth have lower anterior and posterior cingula. *P. carpathicus* Schaub and Zapfe, smallest known species of *Pseudotheridomys*, has a short mesolophid and a distinct ectolophid in lower cheek teeth. *Ligerimys* Stehlin and Schaub has a weak mesoloph although it has a strong mesolophid in lower cheek teeth.

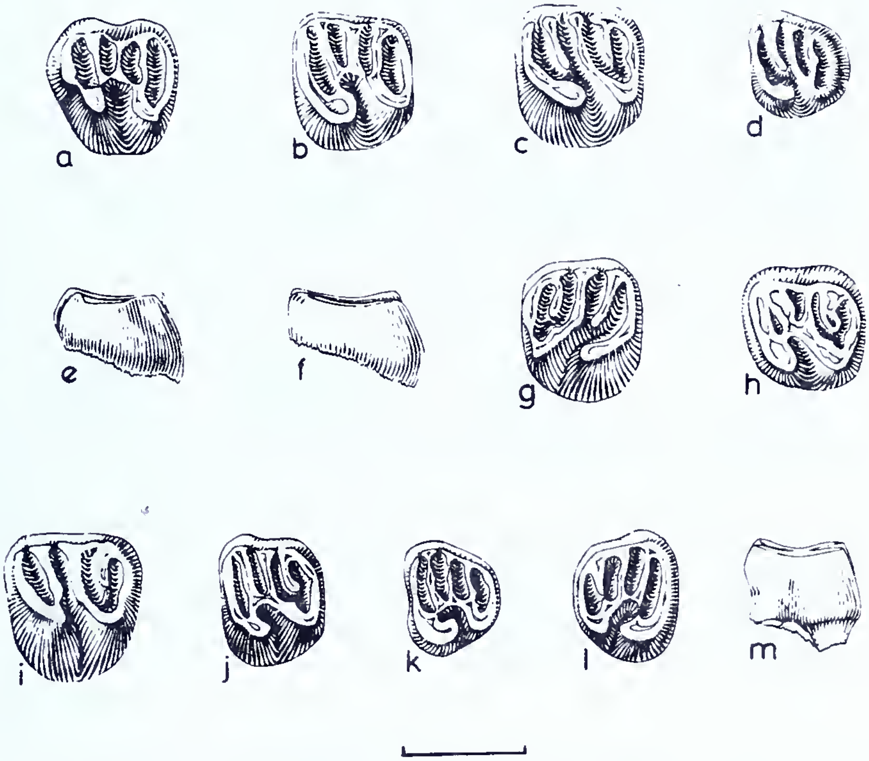

Fig. 3. *Pseudotheridomys cuyamensis* n. sp. a. UCMP 82119, left P^4, occlusal view. b. UCMP 82124, left M^1, occlusal view. c. UCMP 82125, left M^2, occlusal view. d. UCMP 82131, left M^3, occlusal view. e. UCMP 82119, left P^4, anterior view. f. UCMP 82124, left M^1, anterior view. g. UCMP 82118, right M^1, occlusal view. h. UCMP 82114, left P^4, occlusal view. i. UCMP 80315, left P^4, occlusal view. j. UCMP 82127, left M^1, occlusal view. k. UCMP 82130, left M^3, occlusal view. l. UCMP 82133, right M^3, occlusal view. m. UCMP 82114, left P^4, anterior view. Scale line equals 1 mm.

Description: Occlusal outlines of P^4's are subquadrate, slightly wider than long. Occlusal outline of M^1 or M^2 is subrectangular, distinctly wider than long. Occlusal outline of M^3 is obovate, with a straight anterior and a rounded posterior margin. The anterior half of M^3 is wider than the posterior. Five transverse lophs (anterior cingulum, protoloph, mesoloph, metaloph, and posterior cingulum) dominate the occlusal surface of upper cheek teeth, cusps are indistinguishable. Protoloph reaches the protocone in 27 of 30 specimens. Protoloph and mesoloph are weakly connected in 26 of 31 specimens. Mesoloph is long, reaching the labial margin of the tooth in all specimens. Anterior and posterior valleys are consistently closed by high anterior and posterior cingula. Outer valley is closed in 24 of 31 specimens. Crown is relatively high, even though brachydont, due to the height and steepness of anterior and posterior cingula.

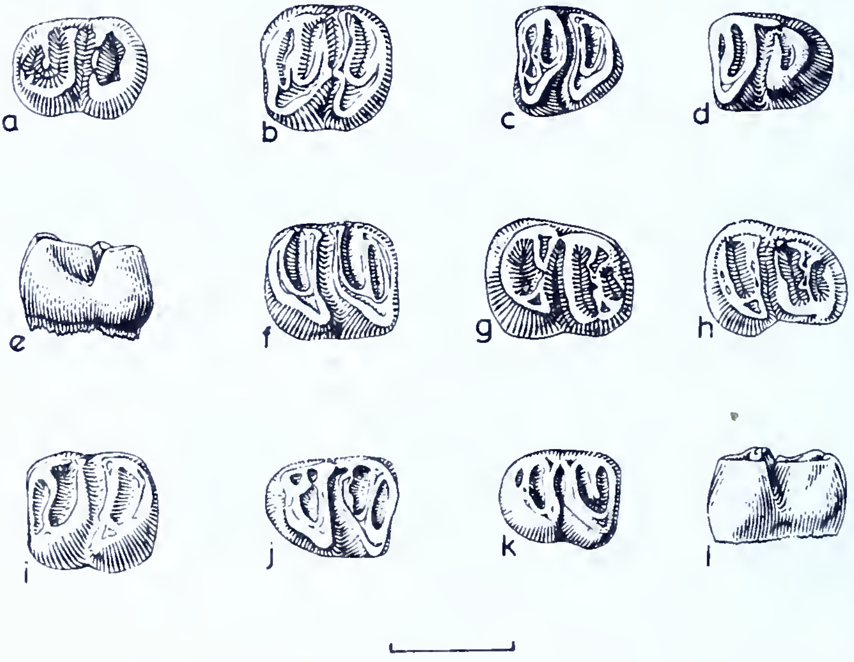

Fig. 4. Pseudotheridomys cuyamensis n. sp. a. UCMP 80320, left P_4, occlusal view. b. UCMP 80317, left M_1, occlusal view. c. UCMP 82107, left M_2, occlusal view. d. UCMP 82103, left M_3, occlusal view. e. UCMP 80320, left P_4, labial view. f. UCMP 82094, right M_2, occlusal view. g. UCMP 82089, right P_4, occlusal view. h. UCMP 80311 (type), right P_4, occlusal view. i. UCMP 82095, left M_1, occlusal view. j. UCMP 82105, right M_3, occlusal view. k. UCMP 82104, right M_3, occlusal view. l. UCMP 80311 (type), right P_4, labial view. Scale line equals 1 mm.

Occlusal outlines of P_4, M_1 and M_2 are subrectangular, longer than wide. M_3 is obovate in occlusal outline, longer than wide, with a straight anterior surface and rounded posterior surface. Anterior half of P_4 is slightly narrower than the posterior, both halves of M_1 are equal in width, and the anterior halves of M_2

and M_3 are wider. Five transverse lophids (anterior cingulum, metalophid, mesolophid, hypolophid, and posterior cingulum) dominate the occlusal surface of lower molars, cusps are indistinguishable. The metalophid is long, reaching the protoconid in all teeth except M_3 in which it reaches the protoconid in 3 of 8 specimens. The metalophid has a medial discontinuity in 3 of 29 specimens. Mesolophid is long, slightly curved, and is continuous from protoconid to lingual border to the tooth in all specimens, with a weak connection between mesolophid and hypolophid in late wear on 20 of 30 specimens. Hypolophid is long, and continuous between entoconid and hypoconid in all specimens. Anterior and posterior cingula are high and steepsided, connecting metaconid-protoconid in all specimens, connecting entoconid-hypoconid in P_4, M_1, M_2 and 3 of 8 specimens of M_3. An anterior lake formed by union of the anterior cingulum and metaconid is narrower, shorter, and shallower than the posterior lake formed by union of the posterior cingulum and entoconid. The lingual border of the tooth is open between entoconid and mesolophid in 24 of 28 specimens, and closed between mesolophid and metaconid in 20 of 26 specimens. Crown is high but brachydont. Anterior and posterior cingula give the false appearance of hypsodonty because of their height and steepness. Base of the crown is rounded, with distinct division between roots and crown. Measurements are given in Table 1.

Discussion: Cheek teeth of *Pseudotheridomys cuyamensis* have high anterior and posterior cingula, and therefore it appears more advanced than *P. hesperus* from Quarry A in Colorado. Cheek teeth of *P. pagei* from Oregon have a better developed mure (ectolophid of Shotwell) than *P. cuyamensis*; it may represent a parallel or later stage of evolution. As suggested by Wilson (1960: 74), *P. hesperus* was probably a new immigrant to North America from Palearctica. *P. cuyamensis* and *P. pagei* were probably derived from *P. hesperus*.

Fahlbusch (1970) recently reviewed European eomyids, recognizing two species, *Pseudotheridomys pusillus* Fahlbusch and *Pseudotheridomys parvulus* (Schlosser), in the late Oligocene-early Miocene of Europe. *P. pusillus* is ancestral to *P. parvulus* and occurs in Chattian age faunas. *P. parvulus* occurs in Aquitanian and Burdigalian age faunas. Either of these European species could be ancestral to the North American immigrant, *P. hesperus*.

Family HETEROMYIDAE Allen and Chapman, 1893

Subfamily Heteromyinae Alston, 1876

Genus *Mookomys* Wood, 1931

Mookomys altifluminus Wood, 1931

TABLE 1. MEASUREMENTS*

		N	$\bar{X}$	S	V	OR
Pseudotheridomys cuyamensis						
P^4	length	9	1.14 ± .02	.068	5.95	1.02-1.22
	width	7	1.18 ± .03	.075	6.35	1.08-1.29
$M^{1,2}$	length	14	0.99 ± .02	.061	6.70	0.90-1.06
	width	12	1.19 ± .02	.066	5.5	1.09-1.24
M^3	length	5	0.85 ± .02	.054	6.35	0.78-0.92
	width	5	0.98 ± .04	.085	8.6	0.89-1.09
P_4	length	7	1.22 ± .01	.036	2.9	1.17-1.26
	width	10	0.95 ± .02	.054	5.7	0.85-0.99
M_1	length	6	1.11 ± .01	.030	2.7	1.09-1.17
	width	4	1.10 ± .01	.018	1.64	1.05-1.14
M_2	length	5	1.04 ± .04	.093	8.94	0.90-1.12
	width	4	0.98 ± .02	.046	4.7	0.92-1.03
M_3	length	8	1.01 ± .03	.087	8.6	0.86-1.12
	width	8	0.90 ± .02	.051	5.7	0.82-0.98
Mookomys cf. *altifluminus*						
P^4	length	2	0.99			0.97-1.00
	width	2	1.16			1.12-1.20
M^1	length	2	1.00			0.96-1.33
	width	2	1.05			0.92-1.18
M^2	length	3	0.92 ± .04	.065	7.0	0.86-0.99
	width	3	1.12 ± .06	.11	9.8	0.99-1.20
M^3	length	5	0.74 ± .02	.038	5.1	0.68-0.78
	width	5	0.92 ± .01	.027	2.9	0.88-0.94
P_4	length	2	0.78			0.66-0.89
	width	2	0.69			0.65-0.73
M_1	length	5	1.06 ± .02	.035	3.3	1.01-1.10
	width	7	1.14 ± .03	.082	7.2	1.05-1.23
M_2	length	4	0.90 ± .03	.068	7.5	0.84-0.99
	width	5	1.08 ± .02	.041	3.8	1.02-1.11
M_3	length	3	0.80 ± .01	.015	1.8	0.79-0.82
	width	3	0.88 ± .03	.059	6.7	0.84-0.95

Table 1. (Cont.)		N	$\bar{X}$	S	V	OR
Proheteromys sulculus						
P^4	length	8	1.37 ± .04	.099	7.2	1.24-1.53
	width	8	1.44 ± .02	.050	3.5	1.37-1.53
M^1	length	4	1.03 ± .04	.074	7.2	0.93-1.11
	width	4	1.37 ± .04	.070	5.1	1.28-1.45
M^2	length	8	1.01 ± .03	.072	7.1	0.93-1.17
	width	7	1.32 ± .02	.055	4.2	1.24-1.42
M^3	length	12	0.85 ± .01	.042	4.9	0.79-0.91
	width	12	1.04 ± .02	.053	5.1	0.92-1.11
P_4	length	10	1.12 ± .02	.048	4.3	1.07-1.23
	width	11	1.14 ± .02	.058	5.1	1.00-1.22
M_1	length	5	1.22 ± .02	.054	4.4	1.17-1.28
	width	4	1.35 ± .02	.036	2.7	1.31-1.39
M_2	length	5	1.10 ± .03	.072	6.5	1.00-1.17
	width	5	1.29 ± .02	.037	2.9	1.24-1.33
M_3	length	14	0.91 ± .02	.065	7.1	0.79-0.98
	width	14	1.04 ± .02	.056	5.4	0.95-1.17
Proheteromys magnus						
M^1	length	7	1.56 ± .03	.082	5.2	1.46-1.70
	width	7	1.90 ± .03	.067	3.5	1.82-2.00
M^2	length	3	1.09 ± .04	.068	6.2	1.04-1.17
	width	4	1.52 ± .02	.031	2.0	1.49-1.56
M^3	length	1	1.30			
	width	2	1.45			1.40-1.50
P_4	length	1	1.69			
	width	1	1.51			
M_1	length	5	1.66 ± .02	.034	2.0	1.62-1.70
	width	5	1.74 ± .02	.040	2.3	1.69-1.79
M_2	length	3	1.55 ± .02	.042	2.3	1.50-1.58
	width	3	1.67 ± .02	.035	2.1	1.63-1.69
M_3	length	2	1.40			1.36-1.43
	width	3	1.45 ± .02	.026	1.8	1.43-1.48

*all measurements in millimeters

Mookomys altifluminus Wood, 1931, Amer. Mus. Novitates 501: 7.

Stratigraphic and geographic occurrence: Deep River Formation, Montana, and Branch Canyon Formation, Santa Barbara County, California.

Age: Hemingfordian.

Mookomys cf. M. altifluminus

Material: 31 isolated cheek teeth (1 dP^4, 3 P^4, 2 M^1, 3 M^2, 5 M^3, 2 P_4, 7 M_1, 5 M_2, and 3 M_3) from UCMP locality V6761.

Emended diagnosis: Small brachylophodont heteromyid rodent with lingual hypostyle on P^4. Lophs of upper molars tend to close lingually after little or moderate wear; lophs of lower molars remain separate until late wear. Anterior cingulum of lower molars is separate from protostylid in early wear. Protolophid of P_4 has two prominent, subequal cusps that are separate until late wear; protolophid and metalophid of P_4 are separate until late wear.

Comparisons: M. altifluminus is larger than Mookomys formicorum Wood and Mookomys subtilis Lindsay, both from younger deposits near Barstow, California. Proheteromys parvus (Troxell) is also very similar but larger than M. altifluminus. Topotypic specimens of M. altifluminus were not available for examination when specimens from the Vedder fauna were studied.

Description: Three specimens of P^4 have an oval occlusal outline, with width greater than length. Protoloph is single cusped, with a median, transversely wide protocone. Metaloph is slightly curved and possesses three cusps (metacone, hypocone, and hypostyle). Union of protoloph and metaloph is medial after late wear. Hypostyle is smaller than other cusps; it is oriented anteroposteriorly and has a slightly anterior position relative to metacone and hypocone. All cusps are joined at their bases.

Upper molars have an oval (wider than long) occlusal outline. M^1 is larger than M^2, which is larger than M^3. Protoloph is wider (laterally) than metaloph, although they are near equal on M^2. Lophs join lingually and medially on M^1 after moderate wear, join lingually on M^2 after early wear, and are joined lingually on M^3 when newly erupted. Transverse valley is shallow, slightly curved on M^1, straight on M^2 and M^3. Protoloph is straight with three cusps (paracone, protocone, and protostyle). Metaloph is slightly curved, with three cusps (metacone, hypocone, and hypostyle); metacone is very minute on M^3. The anterior cingulum on M^1 is directed labially from the protostyle, terminating anterior to the paracone. It is much reduced and discontinuous on M^2 and M^3. Posterior cingulum is continuous from hypostyle to metacone,

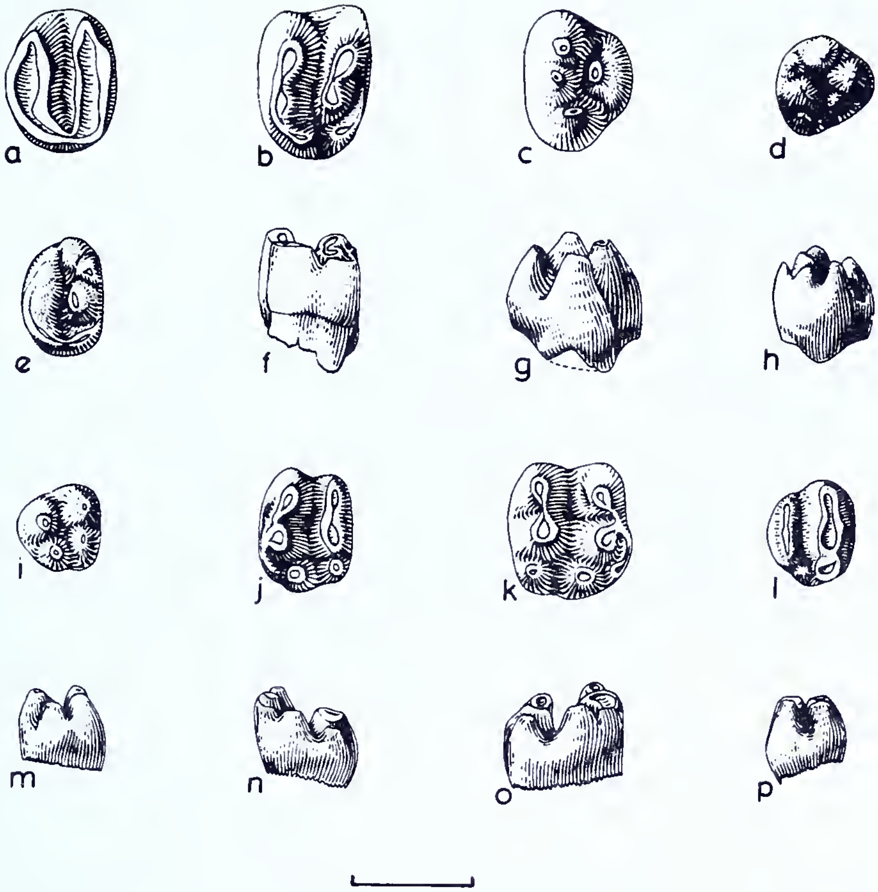

Fig. 5. Mookomys cf. M. altifluminus Wood. a. UCMP 80354, right M^2, occlusal view. b. UCMP 82086, right M^1, occlusal view. c. UCMP 82085, right P^4, occlusal view. d. UCMP 80345, right deciduous P^4, occlusal view. e. UCMP 82069, right M^3, occlusal view. f. UCMP 82086, right M^1, lingual view. g. UCMP 82085, right P^4, anterior view. h. UCMP 80345, right deciduous P^4, anterior view. i. UCMP 82076, left P_4, occlusal view. j. UCMP 82081, left M_2, occlusal view. k. UCMP 82075, right M_1, occlusal view. l. UCMP 82153, right M_3, occlusal view. m. UCMP 82076, left P_4, labial view. n. UCMP 82081, left M_2, labial view. o. UCMP 82075, right M_1, labial view. p. UCMP 82076, left P_4, anterior view. Scale line equals 1 mm.

curving to pass posterior to the hypocone. A median transverse loph (much reduced on M^2 and M^3) connects paracone and protocone.

Two specimens of P_4 have a subcircular occlusal outline. Protolophid is slightly narrower than metalophid, and is oblique to the transverse plane of the tooth. Two separate and subequal cusps (large protoconid and small protostylid) are present on the protolophid. Metalophid is straight with two subequal cusps (metaconid and hypoconid), hypoconid is transversely elongate. The transverse valley is open, protolophid and metalophid do not unite before they are removed by wear.

Lower molar teeth have subrectangular to suboval (wider than long) occlusal outlines. M_1 is larger than M_2, which is larger than M_3. Metalophid and hypolophid are subequal in height and width on M_1, but hypolophid is distinctly lower and narrower on M_2 and M_3. Lophids are never joined until late wear. The transverse valley is open, curved (convex anteriorly) and relatively deep. Metalophid is inflated labially with three principal cusps (metaconid, protoconid, and protostylid) on M_1 and M_2; protostylid is minute on M_3. Hypolophid is straight with three principal cusps (entoconid, hypoconid, and hypostylid) on M_1 and M_2; hypostylid is absent from M_3. The protoconid and hypoconid are near the medial anteroposterior axis of the tooth. Protostylid and hypostylid are smaller than other principal cusps; hypostylid is usually smaller than protostylid. The anterior cingulum unites with the protostylid after moderate wear. It continues lingually on M_1 to terminate anterior to the protoconid; on M_2 and M_3 the anterior cingulum is restricted to the anterolabial corner of the tooth. Entoconid and hypoconid are joined by a low transverse loph. A posteroconid is labial and posterior to the entoconid on 2 of 4 M_1 specimens; it is absent on other molars. Measurements are given in Table 1.

A small unworn dP^4 (UCMP 80345) with subcircular occlusal outline is assigned to M. altifluminus because of its size. Three principal cusps (metacone, protocone, and twinned hypocone) and three secondary cusps (protostyle, hypostyle, and postercone) are present. The metacone is anterolabial, protocone is anterior, and the twinned hypocone is sub-central. These cusps surround a small central valley that opens anterolabially between the protocone and metacone. The protostyle blocks this valley on the anterolingual side and the posterocone blocks the valley on the posterolabial side. Hypostyle is lingual to hypocone.

Discussion: Assignment of this taxon to Mookomys altifluminus is difficult because upper teeth of this species are not known. Specimens of the Vedder fauna assigned to M. altifluminus have a cusp pattern on P^4 that is more characteristic of Heteromyinae than the Perognathinae. As noted by Wood (1931, 1935), Mookomys (the reputed stem of the Perognathinae) is very close to Proheteromys (the stem of the Heteromyinae). Wilson (1960: 78) suggested these subfamilies are not clearly separable at this stage of the Miocene (Hemingfordian).

Nothing in its morphology would exclude M. altifluminus from the ancestry of Proheteromys sulculus, another taxon of the Vedder fauna. Indeed, an earlier population of M. altifluminus probably gave rise to the Vedder M. altifluminus and P. sulculus;

both Mookomys and Proheteromys share characters of the subfamily Heteromyinae. The earliest known heteromyid with a distinctly perognathine cusp pattern on P^4 is Perognathus minutus, known from Barstovian deposits in the Cuyama Badlands and Mojave Desert of southern California.

The deciduous P^4 (UCMP 80345) assigned to M. altifluminus is distinctly heteromyine and has a fairly prominent lingual protostyle. Lingual cusp on the permanent P^4 of Heteromyinae is named a hypostyle, more or less by convention. Morphology of UCMP 80345 suggests the lingual cusp on the permanent P^4 of Heteromyinae may be the protostyle rather than the hypostyle. Rensberger (1971: pl. 8b) illustrated a deciduous P^4 of Heteromys desmarestrianus with a prominent lingual cusp between the protocone and the metaloph as in UCMP 80345. The lingual cusp on permanent P^4 of Heteromyinae should be called a hypostyle until homology can be determined. The lingual cusp on deciduous P^4 of Perognathinae and Dipodomyinae appears to be closer to and connected with the metaloph, and is therefore a hypostyle. Homology of cusps on deciduous and permanent upper premolars of heteromyids may contribute significantly to the understanding of the phylogeny of these subfamilies.

Genus Proheteromys Wood, 1932

Proheteromys sulculus Wilson, 1960

Proheteromys sulculus Wilson, 1960, Univ. Kansas Paleontol. Contrib., Vertebrata 7: 75.

Stratigraphic and geographic occurrence: Pawnee Creek Formation, northeastern Colorado, and Branch Canyon Formation, Santa Barbara County, California.

Age: Hemingfordian.

Material: 79 isolated cheek teeth (11 P^4, 8 M^1, 9 M^2, 12 M^3, 12 P_4, 6 M_1, 7 M_2, and 14 M_3) from UCMP locality V6761.

Description: Upper premolars have an oval occlusal outline with length nearly as great as width. P^4 is larger than upper molars. Protoloph has a single-cusped, transversely oval protocone. Metaloph has two or three cusps (hypocone may be twinned) oriented transversely; paracone and hypocone are connected by a low loph. Hypostyle is lingual, and is usually connected to the metaloph by the posterior cingulum. A small accessory cuspule is anterior to the hypostyle on UCMP 82039 (Fig. 6, a-c). A small posterocone is present on 3 of 10 specimens. The posterior cingulum is arcuate, forming a rounded posterolingual margin of the metaloph in moderate to late wear.

Upper molars have a transversely oval occlusal outline, width

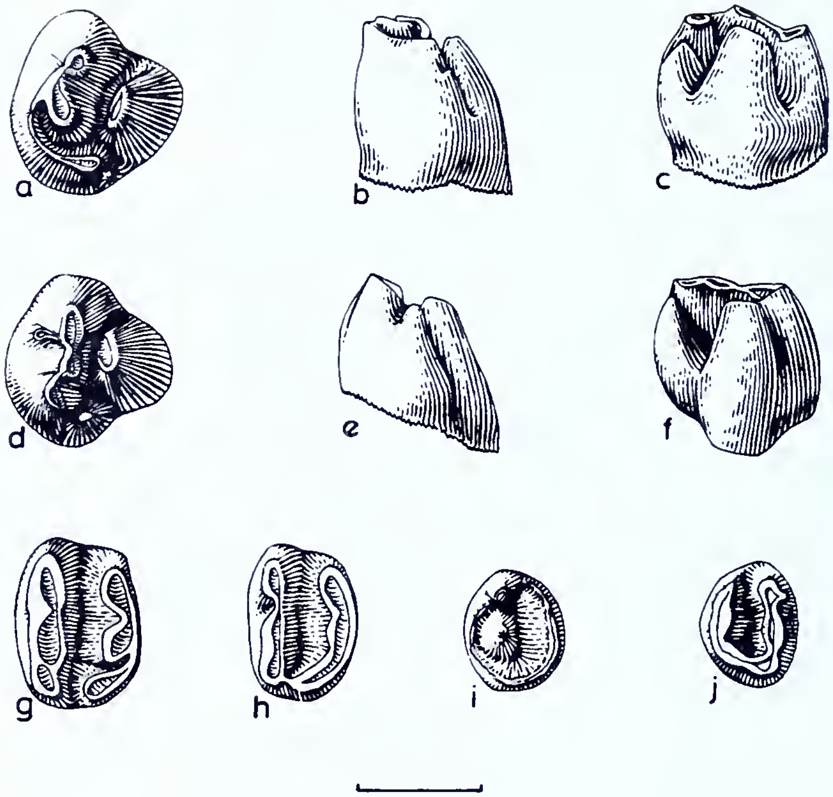

Fig. 6. Proheteromys sulculus Wilson. a. UCMP 82039, right P^4, occlusal view. b. UCMP 82039, right P^4, lingual view. c. UCMP 82039, right P^4, anterior view. d. UCMP 81193, right P^4, occlusal view. e. UCMP 81193, right P^4, lingual view. f. UCMP 81193, right P^4, anterior view. g. UCMP 82043, left M^1, occlusal view. h. UCMP 82051, left M^2, occlusal view. i. UCMP 82061, left M^3, occlusal view. j. UCMP 82068, right M^3, occlusal view. Scale line equals 1 mm.

greater than length. M^1 is larger than M^2, which is larger than M^3. Protoloph is straight with three cusps (paracone, protocone, and protostyle). On M^1 and M^2 the metaloph is curved with three cusps (metacone, hypocone, and hypostyle); on M^3 the hypocone is distinct, hypostyle is indistinct, and metacone is absent. Protostyle and hypostyle are lower than other cusps, except on M^3 where the protostyle is the largest cusp. The transverse valley is narrow and relatively shallow; it is closed lingually by union of protostyle and hypostyle in late wear on M^1, and in early wear on M^2 and M^3. The anterior cingulum is weakly developed, connecting paracone, protocone, and protostyle. The posterior cingulum is well developed, arcuate, connecting the posterior margin of the hypocone with other cusps of the metaloph. A small protoconule is anterior and lingual to the paracone in 5 of 15 specimens of M^1 and M^2, and 8 of 9 specimens of M^3. Posterocone is absent.

Lower premolars have an obovate occlusal outline, length greater than width. P_4 is smaller than M_1. Protolophid is narrower than metalophid and has two cusps (protoconid and protostylid). Metalophid is straight with two large cusps (metaconid and hypoconid) and, on 7 of 11 specimens, a small hypostylid. Protostylid is smaller and slightly posterior relative to the protoconid; these cusps are joined below their apices in 8 of 10 specimens. A small anteroconid is present on one specimen. Protolophid and metalophid are joined submedially in relatively late wear by a low, narrow loph. The transverse valley is deepest on the lingual side.

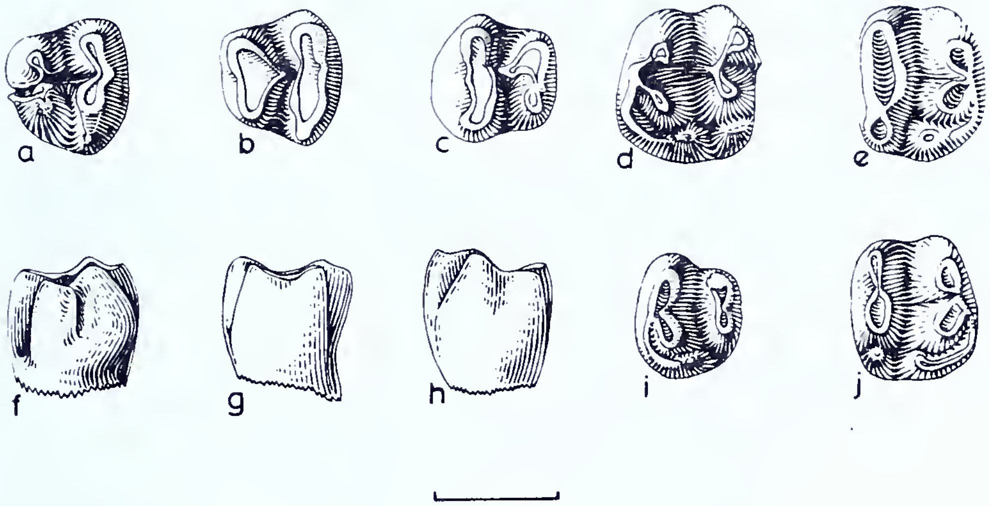

Fig. 7. Proheteromys sulculus Wilson. a. UCMP 82004, left P_4, occlusal view. b. UCMP 82011, left P_4, occlusal view. c. UCMP 82006, right P_4, occlusal view. d. UCMP 80360, left M_1, occlusal view. e. UCMP 82017, right M_2, occlusal view. f. UCMP 82004, left P_4, anterior view. g. UCMP 82011, left P_4, anterior view. h. UCMP 82006, right P_4, anterior view. i. UCMP 82036, left M_3, occlusal view. j. UCMP 80363, right M_2, occlusal view. Scale line equals 1 mm.

Lower molars have an oval occlusal outline, width greater than length. M_1 is larger than M_2, which is larger than M_3. Metalophid and hypolophid are subequal in lateral width on M_1 and M_2; the metalophid is slightly inflated with three cusps, metaconid, protoconid, and protostylid (protostylid is minute or absent on 8 of 10 specimens of M_3). Hypolophid is straight with three cusps (entoconid, hypoconid, and hypostylid) on M_1 and M_2; hypostylid is absent on M_3. Protostylid and hypostylid are smaller than the other cusps, and hypostylid is smaller than the protostylid on M_2. Transverse valley is closed labially or medially in late wear on M_1, closed labially in late wear on M_2, and open until lophs are removed by wear on M_3. Anterior cingulum is prominent on M_1 and M_2, rudimentary on M_3; it is always directed toward the protostylid from the anterior margin of protoconid and metaconid. Posterior cingulum is weakly developed, connecting the entoconid and hypoconid. A small anteroconid is present anterior and labial to the entoconid on another M_1 specimen. Measurements are given in Table 1.

Discussion: *Proheteromys sulculus* is known from two localities, the Quarry A fauna in Colorado and the Vedder Fauna in California. Specimens from Colorado have slightly larger P^4, M^1_3, P_4, and M_3; California specimens have slightly larger M^2 and M^3. Absence of other morphological differences suggests a very close temporal correlation for the Colorado and California assemblages. *Proheteromys floridanus* from the Thomas Farm fauna of Florida is very close to *P. sulculus* but is slightly smaller. It might be interpreted that *P. floridanus* is more primitive than *P. sulculus* because of its smaller size. As stated above, *Mookomys altifluminus* must be close to the ancestry of *P. sulculus*.

Proheteromys magnus Wood, 1932

Proheteromys magnus Wood, 1932, Florida State Geol. Surv. Bull. 10: 46.

Stratigraphic and geographic occurrence: Hawthorn Formation, Florida; Pawnee Creek Formation, Colorado; and Branch Canyon Formation, Santa Barbara County, California.

Age: Hemingfordian.

Material: 34 isolated cheek teeth (1 P^4, 8 M^1, 4 M^2, 2 M^3, 1 dP_4, 2 P_4, 6 M_1, 6 M_2, and 4 M_3) from UCMP locality V6761.

Description: One broken, slightly worn P^4 (UCMP 80330) is assigned to *P. magnus* because of its large size. Its transversely oval protocone is connected lingually to the hypostyle.

Occlusal outline of upper molars is subrectangular (although slightly more oval in M^2 and M^3), wider than long. M^1 is larger than M^2, which is larger than M^3. Protoloph and metaloph are subequal in width on M^1 and M^3, protoloph is slightly wider than metaloph on M^2. Protoloph is straight with three principal cusps (paracone, protocone, and protostyle). Metaloph with three principal cusps (metacone, hypocone, and hypostyle) is curved and inflated medially. Lophs are united lingually in M^2 and M^3 after moderate wear, they are united in M^1 after late wear. Protocone and hypocone are near the median axis of the tooth. Paracone, protocone, and protostyle are connected posteriorly by a low transverse loph in M^1 and M^2, protostyle is isolated in M^3. A

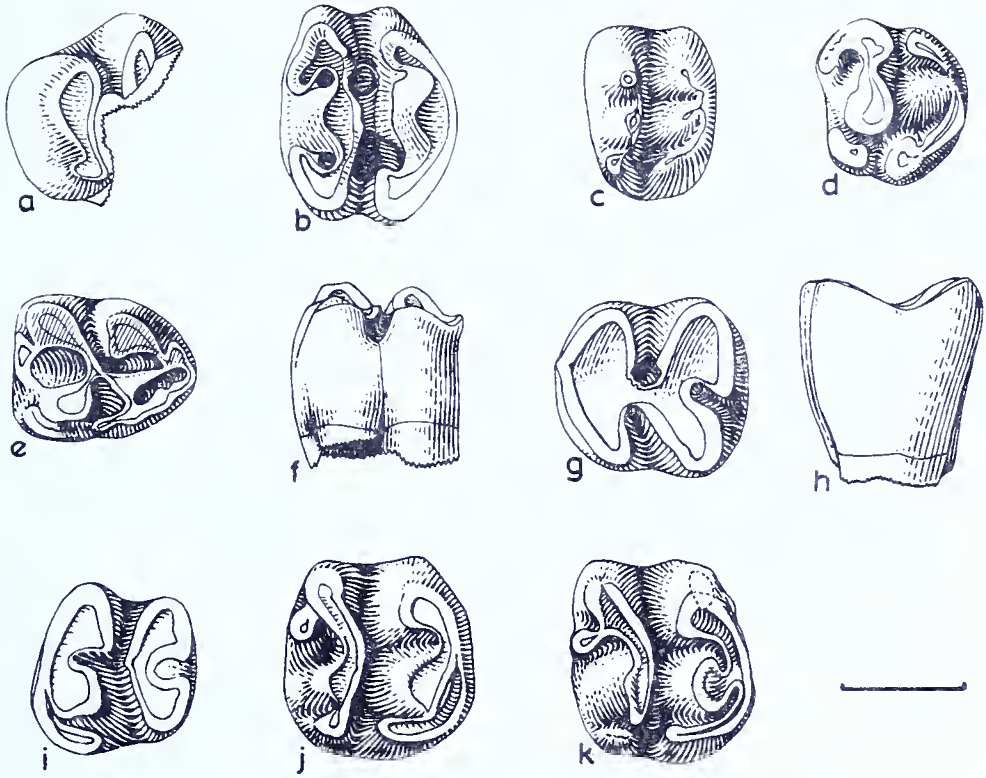

Fig. 8. Proheteromys magnus Wood. a. UCMP 80330, left P^4, occlusal view. b. UCMP 81197, left M^1, occlusal view. c. UCMP 82074, left M^2, occlusal view. d. UCMP 82161, left M^3, occlusal view. e. UCMP 82154, right deciduous P_4, occlusal view. f. UCMP 81197, left M^1, lingual view. g. UCMP 80334, left P_4, occlusal view. h. UCMP 80334, left P_4, anterior view. i. UCMP 82155, left M_3, occlusal view. j. UCMP 80341, right M_2, occlusal view. k. UCMP 80339, right M_1, occlusal view. Scale line equals 1 mm.

posterior cingulum is continuous between the metacone and hypostyle, on the posterior side of the hypocone. A minute to small protoconule is present on 12 of 14 specimens. Union of paracone and protoconule after moderate wear, and triangular shape of the protostyle tend to isolate enamel lakes adjacent to the protocone, especially on M^1. Base of the enamel is deepest on the median anteroposterior axis in M^1.

An isolated deciduous P_4 (UCMP 82154) is assigned to P. magnus because of its size and crown height. Occlusal outline of the tooth is elongate oval, longer than wide. Anterior and posterior lophs are joined by a narrow median loph. Protolophid has a prominent metaconid, distinctive protoconid and protostylid, and a small anteroconid. Metaconid, protoconid, and anteroconid are joined medially by a low loph. Metalophid has a prominent entoconid and hypoconid; posteroconid and hypostylid are small. Entoconid and hypoconid are joined anteriorly by a transverse loph that also joins the median loph. An anterior cingulum is continuous on the labial side from anteroconid almost to hypoconid. Enamel in this specimen is relatively thick, and depth of the crown is approximately twice the height of cusps.

Lower permanent premolars have a subrectangular occlusal outline, longer than wide. Protolophid and metalophid are joined medially by a narrow loph; both lophs have two principal cusps, metaconid and protoconid on the protolophid, entoconid and hypoconid on the metalophid. Transverse valley is closed, very narrow, and moderately deep. A posteroconid and hypostylid are barely discernible. Anteroconid is absent. Depth of the crown is approximately twice the height of the cusps.

Lower molars have subrectangular occlusal outlines. M_1 and M_2 are wider than long, M_3 is approximately as wide as long. M_1 is larger than M_2, which is larger than M_3. Metalophid and hypolophid are always separate until late wear. These lophids are subequal in lateral width on M_1 and M_2, hypolophid is narrower on M_3. Metalophid is inflated labially and has three principal cusps (metaconid, protoconid, and protostylid). Hypolophid is straight with three principal cusps (entoconid, hypoconid, and hypostylid) on M_1 and M_2; hypostylid is absent on M_3. Protoconid and hypoconid are always labial relative to the median anteroposterior axis of the tooth. Protostylid and hypostylid are smaller than other principal cusps. A small to minute posteroconid is present on M_1 and M_2. Anterior cingulum is curved, continuous along the anterior border of the tooth between metaconid and protostylid, and anterior to the protoconid on M_1 and M_2; it is reduced on M_3, terminating anterior to the protoconid. Entoconid, hypoconid, and hypostylid are connected anteriorly by a low transverse loph. Measurements are given in Table 1.

Discussion: *Proheteromys magnus* was described from the Thomas Farm fauna of Florida (Wood, 1932), and a similar but not identical form was described from Quarry A fauna of Colorado by Wilson (1960). *P. magnus* specimens from the Vedder fauna are within the size range of specimens from Florida and Colorado (measurements of Black, 1963) with P_4 slightly larger in the California specimens. Morphologic similarity of *P. magnus* specimens from these three areas suggests very close temporal correlation. Assuming a trend toward large size, *Proheteromys maximus* James (1963) from the Cuyama Badlands is probably derived from *P. magnus*.

ACKNOWLEDGEMENTS

I am very grateful to D. E. Savage for the opportunity to study the Vedder specimens. Several colleagues from the University of California Museum of Paleontology helped in collecting, screen-washing, and picking fossil matrix from the Vedder locality. Especially helpful were D. P. Whistler and J. H. Hutchison. Illustrations were made by staff artist J. Patricia Lufkin of the University of California Museum of Paleontology.

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ERRATA

To PaleoBios No. 15, p. 17. Insert between Age: and Description:

Blackia sp. indet.

Material: UCMP loc. V6761 - UCMP 82137, left M_3; and UCMP 82140, left P^4.

PALEOBIOS

Contributions from the University of California
Museum of Paleontology, Berkeley

No. 17 July 25, 1974

HEPTRANCHIAS HOWELLII (REED, 1946) (SELACHII: HEXANCHIDAE) IN THE EOCENE OF THE UNITED STATES AND BRITISH COLUMBIA

by

Bruce J. Welton

no. 17

HEPTRANCHIAS HOWELLII (REED, 1946) (SELACHII: HEXANCHIDAE) IN THE EOCENE OF THE UNITED STATES AND BRITISH COLUMBIA

BY BRUCE J. WELTON[1]

ABSTRACT

Notidanion howellii Reed, 1946 (Selachii: Hexanchidae) from the Eocene Shark River Formation of New Jersey is referred to the genus *Heptranchias*. Teeth of *Heptranchias* from the Eocene of Vancouver Island, British Columbia, the Lincoln Creek Formation of Washington, and the Keasey and Nestucca Formations of Oregon are considered to be conspecific with *Heptranchias howellii*. *H. howellii* is chronologically restricted to strata of Narizian and lower Refugian age in the northeastern Pacific and is interpreted to be a deep water form, occurring in association with upper bathyal-lower neritic invertebrate faunas.

INTRODUCTION

Gill (1885) defined the family Hexanchidae to include three extant genera, *Hexanchus* Rafinesque, 1810, *Notorhynchus* Ayres, 1855, and *Heptranchias* Rafinesque, 1810. *Hexanchus* and *Notorhynchus* had a cosmopolitan distribution throughout the Cenozoic whereas *Heptranchias* is presently known only from the Oligocene of Japan (Applegate and Uyeno, 1968) and the Eocene of Vancouver Island, British Columbia (Waldman, 1971).

Reed (1946) described *Notidanion howellii*, a new Eocene shark of the family Notidanidae from the Shark River Formation of New Jersey. She stated that "In size, *Notidanion howellii* compares favorably with the Cretaceous and Early Tertiary species of *Notidanion microdon* (Agassiz), *Notidanion serratissimus* (Agassiz), and *Notidanion tenuidens* (Leriche), all of which were originally described as species of *Notidanus*. It differs from *Notidanion microdon* (Agassiz) and *Notidanion serratissimus* (Agassiz) in having the anterior denticles much larger, and in having a different number and arrangement of accessory cones. It differs from *Notidanion tenuidens* (Leriche) in the greater thickness of the root, more numerous anterior denticles and fewer accessory cones" (Reed, 1946: 3).

There is a great similarity between Reed's figures of *N. howellii* and teeth of *Heptranchias* which Waldman (1971) figures from the Eocene of Vancouver Island, British Columbia. Waldman did not compare his specimens with *N. howellii*; however, subsequent examination of his specimens revealed that these two forms are congeneric and probably conspecific.

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[1] Museum of Paleontology, University of California, Berkeley, 94720.

Welton (1972, 1973) described Heptranchias from the late Eocene of Oregon but refrained from making a specific diagnosis. Morphologically the Oregon teeth differ only slightly from N. howellii and I now consider them to be conspecific.

Heptranchias and Hexanchus were defined by Rafinesque in 1810 for sharks having seven and six pairs of gill openings, respectively. Cuvier (1817, 1829) placed both genera in synonomy with Notidanus Cuvier, 1817 (= Notidanion Reed, 1946) in the family Notidanidae. The name Hexanchus has priority over Notidanus, a problem discussed by Applegate (1965b). He demonstrated that each of these genera may be distinguished from the others on the basis of tooth morphology, the lower laterals in particular. Hexanchus may have either a smooth (as in the case of juvenile teeth) or serrated symphysial margin on the primary cusp (Fig. 1E). Heptranchias has one to five distinct narrow denticles on the symphysial margin of the primary cusp (Fig. 1C), and the third genus of Hexanchidae, Notorhynchus, differs in having small unequal denticles (Fig. 1D).

The lower lateral teeth in Hexanchus and Notorhynchus exhibit a large primary cusp and smaller secondary cusps which decrease in height along a gradient from sc_1, sc_2, sc_3 ... to the last cusp (Fig. 1 D, E). Heptranchias (Fig. 1 A-C and Pl. 1) resembles other hexanchids in having a large primary cusp and differs in its ungraduated secondary cusp pattern.

The meagerness of the fossil record of Heptranchias is more apparent than real and is due in part to systematic and taxonomic confusion regarding generic differences in the Family Hexanchidae. For example, in a paper describing the elasmobranch faunas of Australia, Pledge (1967: 140) stated that "Notidanus Cuvier included Hexanchus and Heptranchias Rafinesque 1810, and Notorhynchus Ayres 1855, as there is no apparent generic difference between the teeth of these living genera." Of the four figured hexanchid teeth (Pledge, 1967: pl. 1, figs. 1-3) which he refers to Notidanus serratissimus Agassiz, the lower tooth in fig. 3 belongs to Heptranchias and the remainder are clearly lower laterals of Hexanchus.

Jordan (1907) described Heptranchias andersoni on the basis of four teeth from Barker's Ranch (Hemingfordian), Kern County, California. Leriche (1908) synonymized Heptranchias andersoni with Notidanion primigenius and Arambourg (1927) referred Heptranchias andersoni to Hexanchus gigas. I consider Arambourg's generic assignment to be correct but hesitate to refer the West Coast species to a European taxon (Hexanchus gigas) until the former has been adequately diagnosed.

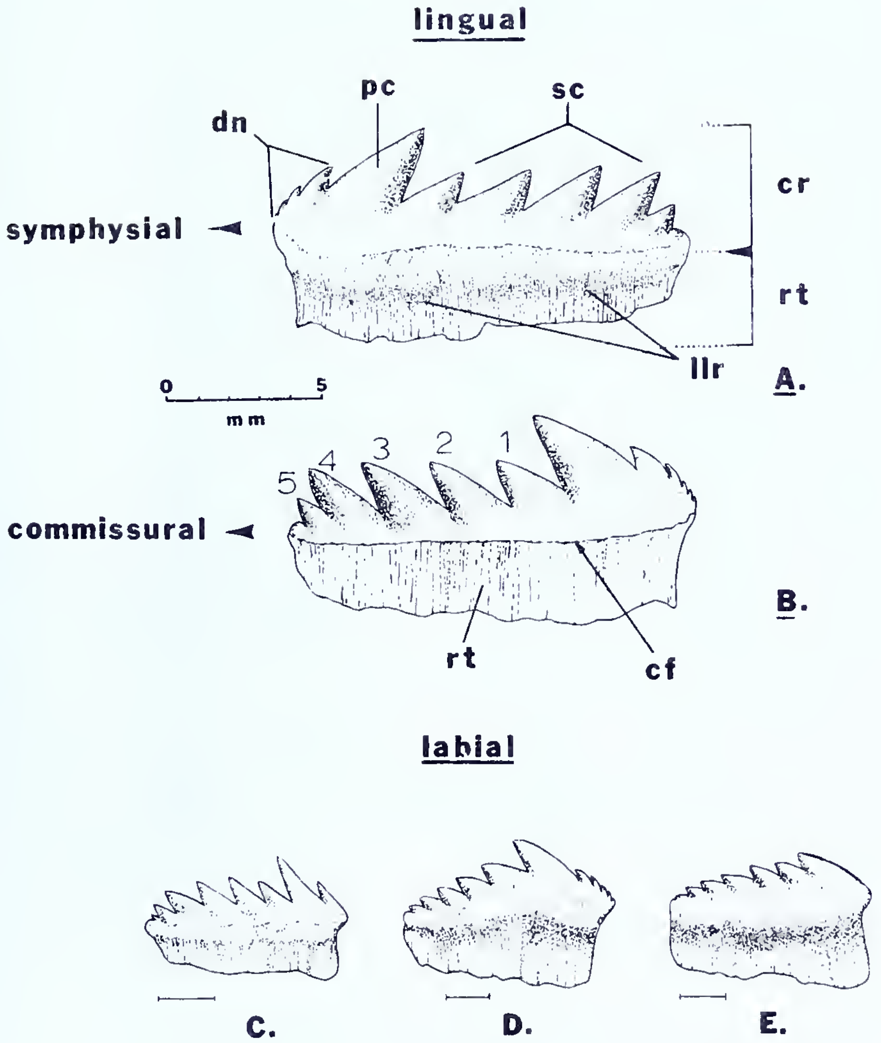

Figure 1. A & B, Heptranchias howellii (Reed, 1946); holotype, ANSP 15078, lower left lateral tooth. C. Heptranchias perlo; LACM F-468, lower left fourth lateral tooth, scale line = 2 mm. D. Notorhynchus maculatus; LACM F-461, lower left fourth lateral tooth, scale line = 4 mm. E. Hexanchus griseus; LACM F-107, lower left fourth lateral tooth, scale line = 4 mm. Abbreviations: cf, crown foot; cr, crown; dn, denticles; llr, longitudinal lingual ridge; pc, primary cusp; rt, root; sc, secondary cusps, numbered one through five.

PLATE 1. Heptranchias perlo, LACM F-468, collected in Suruga Bay, Shizuoka, Japan; upper and lower left tooth series: lacking L^7 in the upper series and posteriors in both upper and lower series. Abbreviations: A, anterior; L, lateral; M, medial; S, symphysial; scale line = 5 mm.

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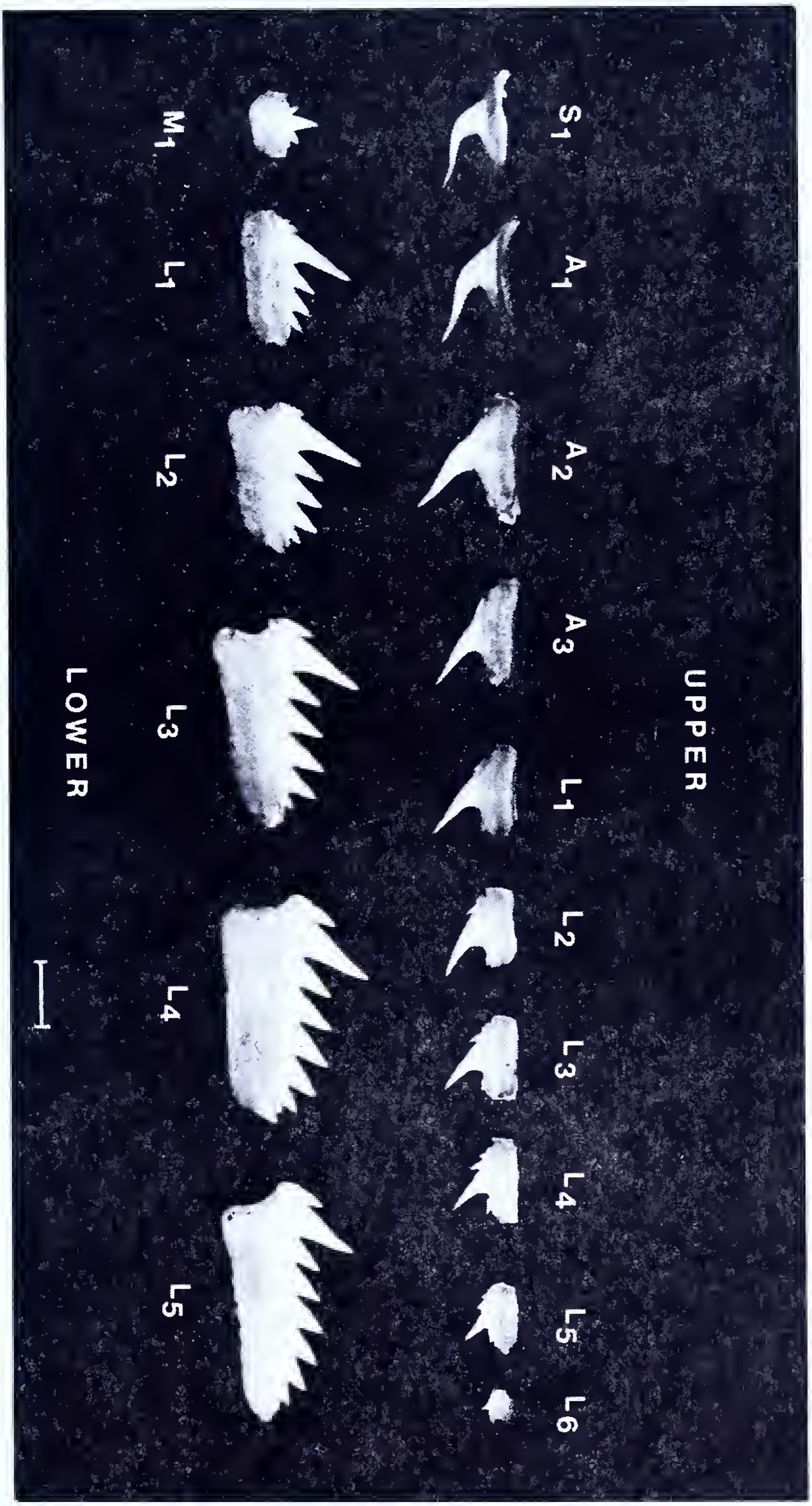

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It is the purpose of this paper to reconsider the species *Notidanion howellii* Reed, 1946 and to discuss its chronologic, biogeographic and paleoecologic occurrence in the Eocene of western Oregon, Washington, and Vancouver Island, British Columbia.

ABBREVIATIONS

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; GSC, Geological Society of Canada, Ottawa; LACM, Natural History Museum of Los Angeles County, Vertebrate Paleontology Section; NSMT, National Science Museum, Tokyo, Japan; PSU, Portland State University, Earth Sciences Museum, Portland, Oregon; UCMP, University of California Museum of Paleontology, Berkeley; UW, Burke Memorial Washington State Museum, Division of Geology and Paleontology, University of Washington, Seattle; CR-7, UW-CR-6, locality numbers used in unpublished text of John M. Armentrout's (1973) University of Washington Ph.D. dissertation.

The tooth terminology used in this paper is based in part upon Applegate (1965a) and Compagno (1970), and is illustrated in Fig. 1 A and B.

ACKNOWLEDGEMENTS

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SYSTEMATICS

Order HEXANCHIFORMES Berg, 1940

Family HEXANCHIDAE Gill, 1885

Genus *Heptranchias* Rafinesque, 1810

(Figure 1A, B, C; Plates 1, 2)

Diagnosis: Teeth different in upper and lower jaw, with upper anteriors bearing a single commissurally flexed primary cusp lacking symphysial denticles or secondary cusps; teeth strongly different between lower M_1 and L_1 and between laterals and postteriors of both upper and lower series; lower labials comb-like with a high primary cusp, one to five denticles on the symphysial edge of the primary cusp, and four to nine secondary cusps of ungraduated height; upper laterals smaller than lowers with a single primary cusp, one or two secondary cusps and one or two symphysial denticles; length of crown foot and denticle number increase in size toward commissure in upper laterals; roots undivided, tabular except in posteriors which are dorsoventrally depressed and small; lower and upper posteriors simple, extremely small, elongate with low crown which lacks cusps.

Type Species: Heptranchias cinereus Rafinesque, 1810

Heptranchias howellii (Reed, 1946), new combination

Notidanion howellii Reed, 1946, Notulae Naturae Acad. Nat. Sci. Philadelphia 172: 1-3.

Revised Description of Holotype: Lower left ?fourth lateral tooth possessing five denticles on the symphysial edge of the primary cusp near the crown base. The denticles increase gradually in size toward the cusp apex. The primary cusp is twice as large as sc_1, broad at its base with straight symphysial and commissural edges; and is followed by five secondary cusps; sc_1 and sc_2 are equal in height, sc_3 and sc_4 are taller than the latter two and also equal in height, sc_5 is one third the height of sc_4. The denticles, primary cusp and secondary cusps are inclined commissurally at an angle of approximately fifty degrees. A horizontal line is formed on the lingual tooth surface by the junction of the crown foot and root. A rounded transverse lingual ridge extends the length of the root, approximately 1 mm below the crown base, bending slightly upward at the commissural end and terminated at the symphysial border by a slight dorsoventral depression. The root is tabular, somewhat rectangular and dorsoventrally narrowed toward the commissural end. In cross section the root is wedge-shaped, thickest at its junction with the crown base and tapering toward the posterior root border. The tooth is flat on the labial side, lingually convex. All cusps lack serrations and are "so thin as to be almost translucent; the tooth as a whole is slightly twisted, but the cusps and denticles are set straight on the root, and are not at all sigmoid" (Reed, 1946).

Measurements: Total height 7 mm (measured from the tip of the primary cusp to the root base, perpendicular to the ventral margin of the root); total length 13 mm (measured from the symphysial to commissural margins along the crown foot).

Discussion: Heptranchias howellii differs from H. ezoensis Applegate and Uyeno, 1968, NSMT 7421, in having narrower cusp bases, a narrower and high primary cusp and more than two denticles on the symphysial edge of the primary cusp. A higher primary cusp and the presence of no more than three denticles on the lower lateral teeth differentiates the extant species *H. perlo* (Bonnaterre, 1788) from *H. howellii*.

The Hexanchidae have well developed heterodonty, both along a single tooth series and between upper and lower jaws, with medial, symphysial, anterior, lateral, and posterior tooth types (Applegate, 1965a). *Heptranchias perlo* has the following dental formula:

LACM F-468, Male:

$$\text{Left}\quad \frac{\text{P10 L7 A3 S1 S1 A3 L7 P11}}{\text{P11 L5 M1 L5 P14}}\quad \text{Right}$$

Tooth positions L_1 through L_5 in the lower dentition of *Heptranchias perlo* (Plate 1) are distinguished by the size and number of cusps, number and arrangement of denticles, height and width ratios, and root morphology. Teeth in the females of *H. perlo* bear a larger number of secondary cusps than in males of the species (Bigelow and Schroeder, 1948). Confirmation of the presence or absence of this dimorphism in *H. howellii* and the accuracy of my interpretations of the tooth positions must await the examination of additional specimens when arranged in tooth sets.

OCCURRENCES OF *HEPTRANCHIAS HOWELLII*

Among the Tertiary selachian assemblages from Oregon, Washington, and British Columbia in the collections at Portland State University, the University of California Museum of Paleontology at Berkeley, the Burke Memorial Washington State Museum, and the Geological Survey of Canada, are six teeth which are referable to *Heptranchias howellii*.

Oregon

Referred Specimens: PSU F-419, first lower left lateral tooth; UCMP 57456, fourth lower left lateral tooth (Plate 2B).

Formation and Age: Middle member of the Keasey Formation (Schenck, 1927; Warren and Norbisrath, 1946), Lower Refugian (Upper Eocene).

Locality: UCMP loc. V6730, 5' above base of a prominent bluff, during the August low water stage, on W side of Nehalem River, immediately S of the Burn Road Bridge, 0.3 miles S of junction of Oregon State Highways 47 and 202 at Mist, Oregon: NE 1/4 NE 1/4 SE 1/4 Sec. 23, T5N, R5W, Birkenfield Quadrangle (15', 1955), Columbia County, Oregon.

Referred Specimen: PSU F-426, lower right fifth lateral tooth (Plate 2A).

Formation and Age: Nestucca Formation (Snavely and Vokes, 1949), lower Narizian (Bulimina corrugata zone of Mallory, 1959).

Locality: 10' above beach and approximately 100' below a 400' thick flow of basalt, on N shore of Salmon River at Cascade Head, 1/4 mile from mouth of the Salmon River and the Pacific Ocean and 304' N of Teal Creek, in NW 1/4 SE 1/4 Sec. 14, T5S, R11W, Hebo Quadrangle (15', 1955), Tillamook County, Oregon.

Washington

Referred Specimen: UW 60692, anterior half (denticles, primary cusp and sc_1, sc_2) of a lower right lateral tooth with mold of sc_3 - sc_5.

Formation and Age: Lincoln Creek Formation, Echinophoria dalli zone, lower Refugian.

Locality: UW-B0268, Canyon River Section, traverse up-section along the Canyon River from the north in Sec. 18, T21N, R6W, toward the south to Sec. 36, T21N, R6W, Mt. Tebo and Grisdale Quadrangles, (15', 1953), Mason and Grays Harbor Counties, Washington; Loc. CR-7, glauconitic silty sandstone; 3' thick bed with thanatocoenose fauna, in glauconite sand 6' stratigraphically above Loc. UW-CR-6, just above deep pool at SE corner of meander bend, 4700' W, 800' N of SE corner, Sec. 18, T21N, R6W (Personal communication, J. Armentrout, 1974).

Vancouver Island, British Columbia

Referred Specimens: GSC No. 21734 A and GSC No. 21734 B, two lower lateral teeth.

Formation and Age: Jeletzky's "Division C" of Unit 2 of the Tertiary beds of the Hesquiat Peninsula, Vancouver Island (Waldman, 1971), lower Refugian (Sigmomorphina schencki zone) (Cameron, 1971).

Locality: "West coast of Vancouver Island, British Columbia, east side of Hesquiat Peninsula, 0.6 miles (1 km) south of Hesquiat village, 20 yards (18 m) from the beach below high water mark (Waldman, 1971)."

Measurements

Specimen Number	Total Height	Total Length
PSU F-419	3.4 mm	6.0+ mm
PSU F-426	7.5+ mm	15.4+ mm
UCMP 57456	9.9 mm	17.0+ mm
UW 60692	9.1+ mm	6.1+ mm
GSC 21734A	-	19.0 mm (Waldman, 1971)
GSC 21734B	-	25.0 mm (Waldman, 1971)

CHRONOSTRATIGRAPHIC DISTRIBUTION OF HEPTRANCHIAS HOWELLII

H. howellii is a minor but characteristic element of the Eocene deep water fish faunas from western Oregon and Washington and southwestern British Columbia. Its chronostratigraphic distribution is presently restricted to strata of Narizian-Refugian age (Fig. 2). Heptranchias howellii first appears in the Bulimina corrugata zone within the upper part of the middle member of the Nestucca Formation (stratigraphic division based upon unpublished data, personal communication, A. D. Callendar, 1974) and its latest occurrence falls within the Sigmomorphina schencki zone of lower Refugian age. This last biostratigraphic zone is represented in stratigraphic Division "C" of Jeletzky (1954) at Hesquiat Peninsula on Vancouver Island, British Columbia, within the lower Lincoln Creek Formation of southwestern Washington (personal communication, J. M. Armentrout, 1973) and perhaps in the upper middle member of the Keasey Formation, Columbia County, Oregon (Fig. 2).

BIOGEOGRAPHY AND PALEOECOLOGY

Upper bathyal to lower neritic sediments of late Eocene age were deposited along the western margin of a tectonically active trench in western Oregon, Washington, and British Columbia (Snavely and Wagner, 1963). Regional subsidence is correlated with the subsequent appearance of bathyal and neritic molluscan, foraminiferal and selachian faunas. The similarity of inferred depositional environments between the Nestucca, Keasey, Lincoln Creek and Vancouver Island sediments (Jeletzky's Division "C") and suggested chronostratigraphic correlation between these formations (Fig. 2) supports this view.

Heptranchias howellii appears to be a geographically limited and narrowly adapted member of the bathyal-neritic fauna in the North Pacific Ocean.

Heptranchias perlo occurs today in waters of the north Atlantic, off South Africa, Australia, and Japan. It is generally considered to be a bottom feeding deep water shark and has been reported at depths of 380 to 460 meters off Portugal and from deep water off Cuba (Bigelow and Schroeder, 1948: 91).

If Heptranchias is indeed a deep water genus then it is not surprising that it should appear in the aforementioned deposits. Moore and Vokes (1953) cited both faunal and lithologic characteristics of the Keasey Formation as indicative of a depth of deposition between 600 and 3,000 feet. A specific depth of 365 m was proposed for the Keasey Formation at Mist, Oregon (UCMP V6730) by Zullo et al. (1964). Welton (1973) listed a selachian fauna for the Keasey Formation at Mist, Oregon that included Notorhynchus, Isurus, Odontaspis, Centrophorus, Squatina, and Pristiophorus. With the exception of Isurus, all of the above taxa are known, on the basis of extant species, to inhabit depths equal to or greater

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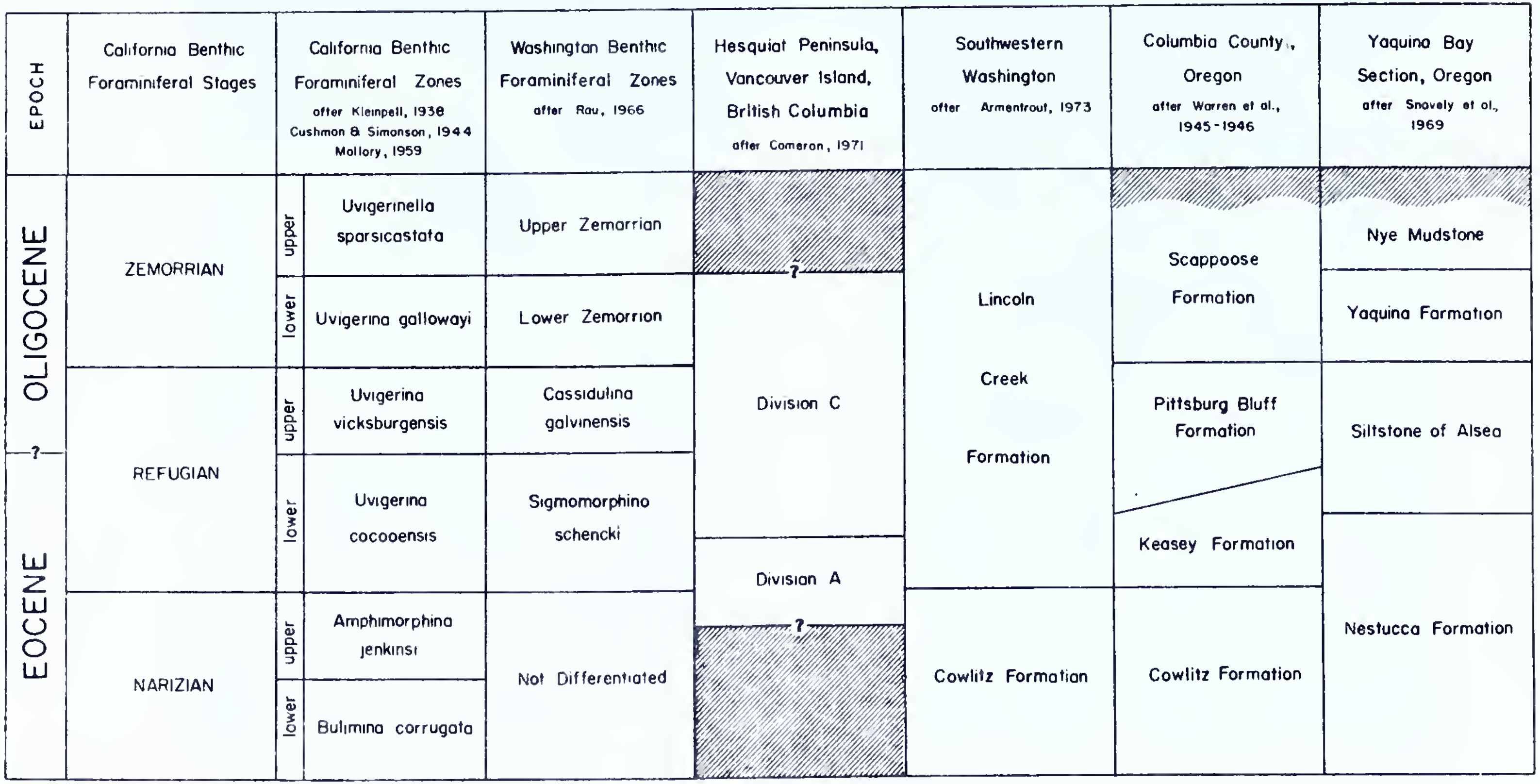
EPOCH
OLIGOCENE
?
EOCENE
California Benthic Foraminiferal Stages
ZEMORRIAN
REFUGIAN
NARIZIAN
California Benthic Foraminiferal Zones after Kleinpell, 1938 Cushman & Simonson, 1944 Mallory, 1959
upper
Uvigerinella sparsicastata
lower
Uvigerina gallowayi
upper
Uvigerina vicksburgensis
lower
Uvigerina cocooensis
upper
Amphimorphina jenkinsi
lower
Bulimina corrugata
Washington Benthic Foraminiferal Zones after Rau, 1966
Upper Zemarrian
Lower Zemorrion
Cassidulina galvinensis
Sigmomorphina schencki
Not Differentiated
Hesquiat Peninsula, Vancouver Island, British Columbia after Cameron, 1971
?
Division C
Division A
?
Southwestern Washington after Armentrout, 1973
Lincoln Creek Formation
Cowlitz Formation
Columbia County, Oregon after Warren et al., 1945-1946
Scappoose Formation
Pittsburg Bluff Formation
Keasey Formation
Cowlitz Formation
Yaquina Bay Section, Oregon after Snavely et al., 1969
Nye Mudstone
Yaquina Formation
Siltstone of Alsea
Nestucca Formation

Figure 2. Correlation chart of stratigraphic units discussed in text.

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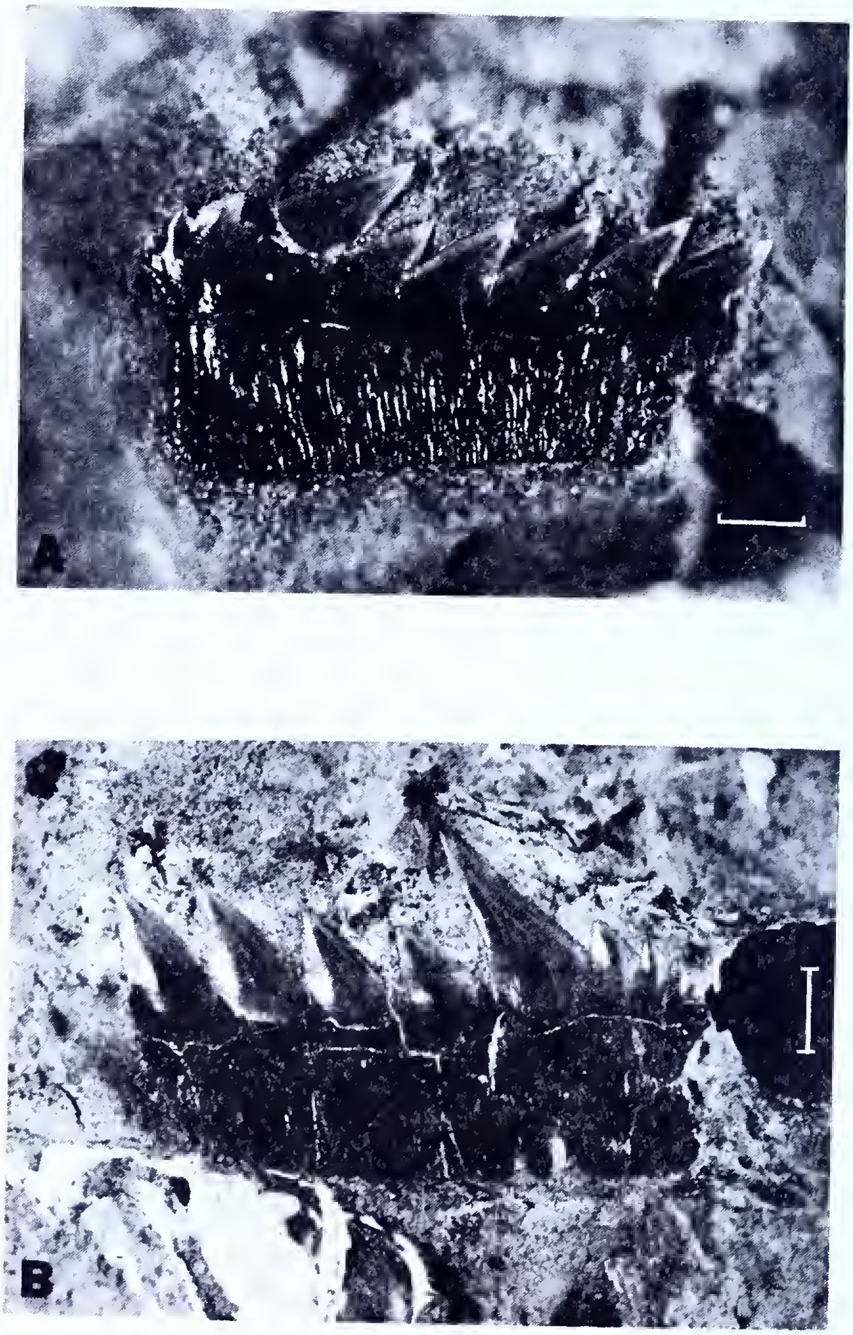

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PLATE 2. A. Heptranchias howellii, PSU F-426, Nestucca Formation, Tillamook County, Oregon; scale line = 2 mm. B. Heptranchias howellii, UCMP 57456, Keasey Formation, Columbia County, Oregon; scale line = 2 mm.

than 365 m. Armentrout (personal communication, 1973) interpreted the Lincoln Creek Formation at UW locality B-0268 as deposited in middle neritic depths of 30 to 100 fathoms with open marine circulation. The Nestucca Formation of Oregon, at Cascade Head, may have been deposited in waters from 600 to 6,000 feet in depth. This is based upon molluscan and foraminiferal evidence (personal communication, A. D. Callendar, 1974). Cameron (1971) interprets Jeletzky's stratigraphic Division "C" on Hesquiat Peninsula, Vancouver Island, British Columbia, as a deep water deposit.

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PALEOBIOS

Contributions from the University of California
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No. 18 July 10, 1975

PATHOLOGY OF TWO FOSSIL SEA COWS (MAMMALIA: SIRENIA)

by

Daryl P. Domning and Fredric L. Frye

PATHOLOGY OF TWO FOSSIL SEA COWS (MAMMALIA: SIRENIA)

BY DARYL P. DOMNING[1] AND FREDRIC L. FRYE[2]

ABSTRACT

Pathological conditions in two fossil sirenian skeletons from California include imperfectly healed fractures, osteomyelitis, and ossifying spondylosis in *Metaxytherium jordani* (Late Miocene), and an unidentified condition grossly resembling osteitis deformans or osteitis fibrosa in *Hydrodamalis sp. nov.* (Late Pliocene). This is the first natural occurrence of osteomyelitis noted in a sirenian.

INTRODUCTION

In recent years numerous specimens of fossil sirenians, including ancestors of the recently (*ca.* 1768) exterminated Steller's sea cow, *Hydrodamalis gigas* (Zimmermann, 1780), have been found in the North Pacific region (Domning, 1975). Among these ancestral forms are two skeletons from California showing particularly interesting and extensive pathological conditions. Both are deposited in the University of California Museum of Paleontology, Berkeley (UCMP).

Metaxytherium jordani KELLOGG, 1925

An old adult individual (4.32 m long) of *Metaxytherium jordani* (UCMP 77037), from the Late Miocene (Clarendonian, Cierbo-Neroly, or Mohnian-Delmontian in West Coast provincial biostratigraphic chronologies; Domning, 1975) Santa Margarita Formation of Santa Cruz County (UCMP locality V6376), shows several types of osteopathology.

The corresponding zygapophyses on the right sides of thoracic vertebrae 7-8 and the left sides of T10-11 are vestigially developed. Caudal vertebrae at the base of the flukes (especially caudals 13-15) show ossifying spondylosis in the form of lipping of the centra, probably as a result of frequent flexion at this point in the tail. The lips do not cross joints but are recurved over the centra bearing them.

The same individual suffered a series of fractures, some exhibiting evidence of osteomyelitis, of the rostrum, sternum, and

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ribs. Most of these exhibit exuberant callus formation.

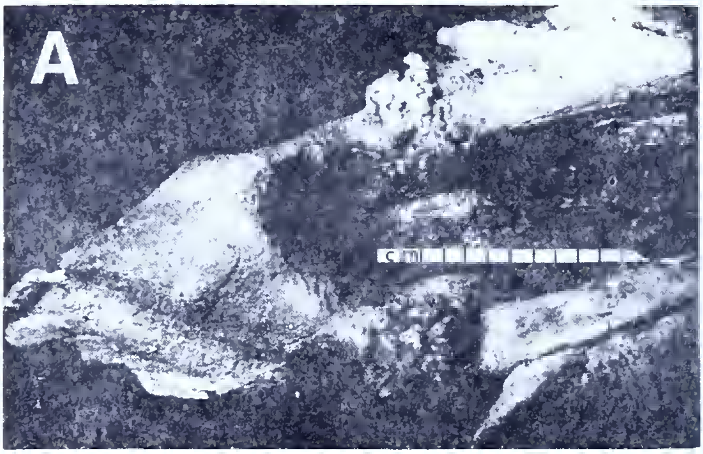
The base of the rostrum (Plate 1A) was completely fractured through the premaxillae and maxillae along an anteroventrad-sloping plane (suggesting a blow from beneath), and had partly healed with development of large carious exostoses and necrotic sinuses on the premaxillae and an irregular hole about 2.5 cm in diameter in the center of the palatal surface. The premaxillae are incompletely healed, the maxillae not at all healed; the rostrum is deflected slightly to the left.

A fracture in the midsection of the left eleventh rib (Plate 1B) has formed some callus and a pseudarthrosis whose surface passes ventrolaterad; wide dorsad-directed lips have formed on the medial sides of both portions. Fractures of the right twelfth and possibly left fifth and sixth ribs have completely healed, forming smaller amounts of callus.

The xiphisternum is transversely fractured about 6 cm from its junction with the manubrium. Its dorsal side has completely healed, but its ventral side shows severe osteomyelitis with large open necrotic sinuses extending onto the ventral and even dorsal sides of the posterior end of the manubrium (Plate 1C, D). The two sternal segments are not fused, possibly as a result of this infection. The sternum is bent sharply upward at the site of the fracture, the anterior and posterior parts of the xiphisternum forming a 235° angle on the dorsal side (Plate 1D).

Anatomical apposition in most of these fractures appears to have been adequate for normal function. Exceptions are the sternebral and eleventh rib fractures, which in the former case healed with marked displacement, and in the latter, healed with a well-developed pseudarthrosis. A non-union involving a weight-bearing long bone would usually create some degree of dysfunction, whereas such a lesion affecting a rib or sternebra may be essentially asymptomatic except for moderate anatomical distortion.

These injuries may have been caused by the animal's being thrown against rocks by surf. Steller (1899:198) observed of *Hydrodamalis gigas* that sometimes "they get caught among the rocks and are dashed by the waves violently upon them". As the Late Miocene species probably depended significantly on kelp for food and therefore, like *Hydrodamalis*, spent considerable time feeding near rocky shores (Domning, 1975), this would not have been an unlikely occurrence. A large wave, lifting the animal and dropping it onto jagged rocks, could have caused the upward displacement of the snout and sternal fractures and the inward displacement of the broken ends of the ribs, as well as wounds open to infection. The injuries could all have occurred in a single accident, or in similar accidents at different times.



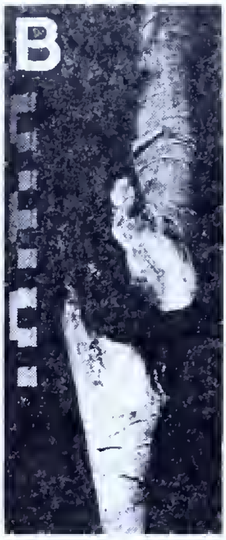
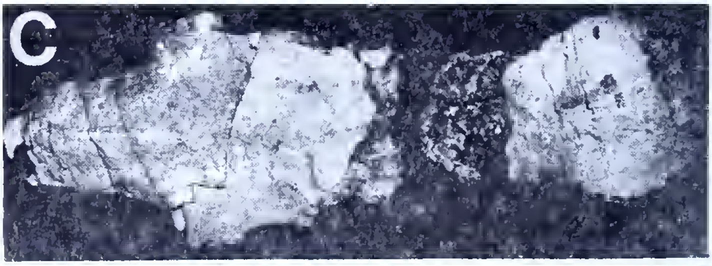
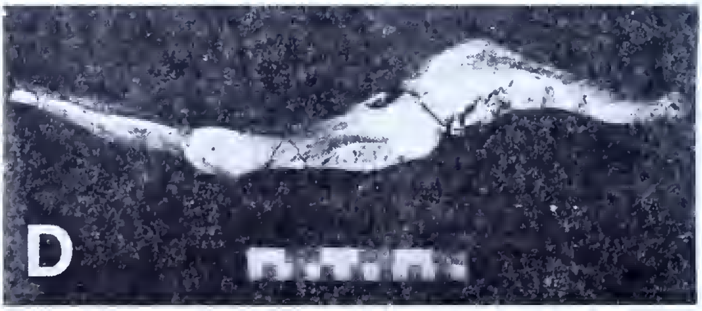


Plate 1. Lesions in skeleton of *Metaxytherium jordani* (UCMP 77037). A. Dorsolateral view of rostrum, showing exostoses on premaxillae. B. Anterior view of pseudarthrosis in left eleventh rib, parts separated. C & D. Ventral and left lateral views of sternum, showing necrotic sinuses on ventral side and sharp bend in xiphisternum. In C manubrium and xiphisternum are slightly separated. Scales in centimeters and inches.





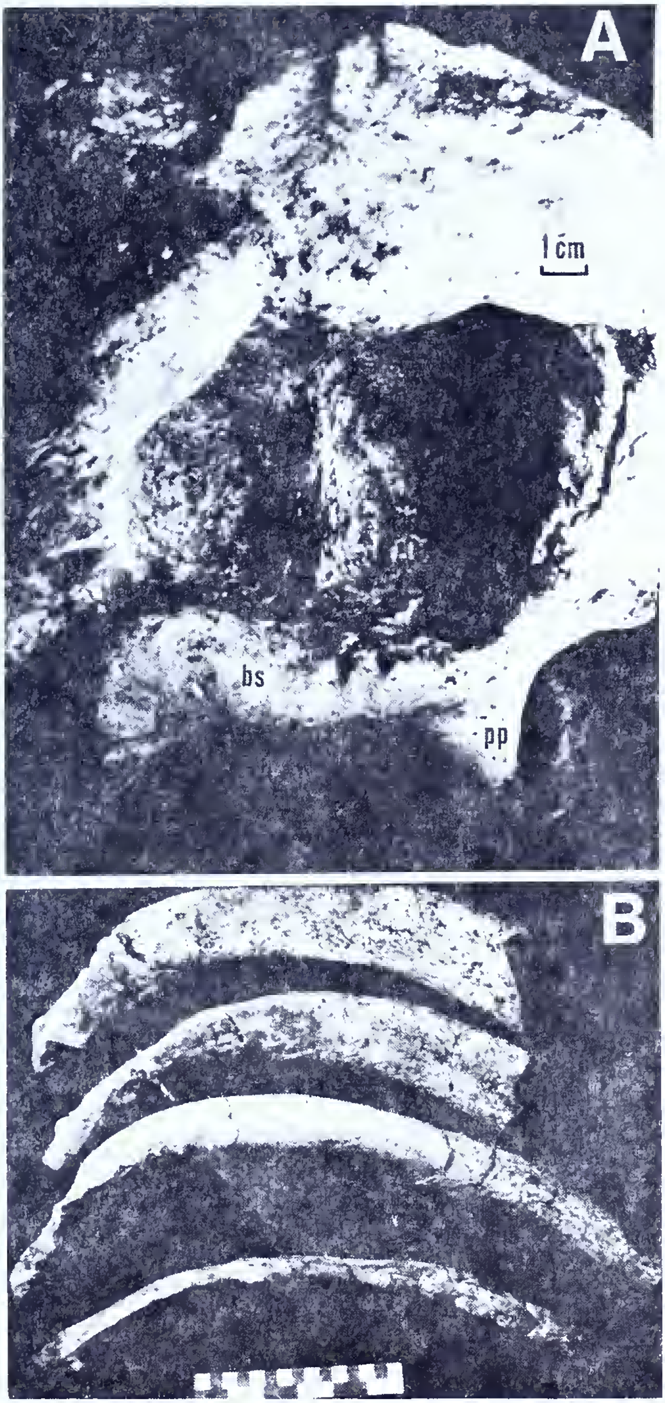


Plate 2. Lesions in skeleton of *Hydrodamalis* sp. nov. (UCMP 86433). A. Posterior view of skull lacking basioccipital and right exoccipital, showing dorsoventral thinness and pitting on dorsal side of basisphenoid (bs), and atrophied condition of pterygoid processes (pp) (tips broken). B. Proximal parts of ribs; top to bottom: posterior views of right ribs 6, 8, and 11, and anterior view of left posterior rib; showing pitting and thinning of proximal ends or (on left rib) entire shaft.

Although fractures (of unknown cause) have been reported in manatees and dugongs (Loth, 1940; Korschelt, 1932; Freund, 1904; Crane, 1881), and human-inflicted wounds caused osteomyelitis in a manatee (Frye and Herald, 1969), this is the first record of naturally-occurring osteomyelitis in a sirenian, as well as of ossifying spondylosis in a form other than fusion of vertebrae. The latter condition, as well as abnormalities of zygapophyses, has already been noted by Reinhart (1959) in a specimen of *Metaxytherium jordani* (his *Halianassa vanderhoofi*; for synonymy see Domning, 1975). The latter specimen, UCMP 3794, came from the same area and stratigraphic unit as UCMP 77037, but it would be unwarranted to conclude from the available sample of this local population (one complete and three partial skeletons and many isolated bones) that the incidence of pathology was unusually high, especially in view of the lack of data on incidence of pathology in Recent sirenian populations. One case of fusion of two thoracic vertebrae and of the dorsal halves of the corresponding left ribs has been noted in *Hydrodamalis gigas* (Pales, 1930: pl. 27, fig. 2); similar conditions probably also occur in *Dugong* and *Trichechus*, but no records have come to our attention.

Hydrodamalis sp. nov.

The second individual is an immature *Hydrodamalis* (UCMP 86433) of a new species which will be described by Domning in the near future; this specimen is from the Late Pliocene (Blancan; Domning, 1975) Squire Member of the Pismo Formation, San Luis Obispo County (UCMP locality V70148). It suffered from an unidentified disabling affliction of bones, joints, and muscles of the jaw, neck, and back regions. Bone resorption, leaving irregularly pitted surfaces, has taken place on the dorsal side of the basisphenoid (Plate 2A), on the proximal ends of right ribs 4, 6, 8, and 11 (the intervening ribs are almost or entirely unaffected; the corresponding left ribs are not preserved), and on the entire lengths of several posterior left ribs (Plate 2B). Cervical vertebrae 2 and 3 are fused on the left side; the right side of C3 was evidently partly resorbed. The pterygoid processes and basisphenoid (Plate 2A) and the dorsolateral border of the exoccipital show subnormal growth and thickness, suggesting atrophy of the attached muscles (pterygoidei, longus capitis, and semispinalis capitis, respectively). The rostrum and the posterior parts of the mandibles show no abnormalities, but the anterior ends of the latter, though only partly preserved, seem to have tapered rather abruptly instead of showing the expected robust development of the symphyseal region, suggesting atrophy possibly attributable to the weakness of the pterygoid muscles.

Although the lesions grossly resemble those of osteitis deformans or osteitis fibrosa, these could not be distinguished on the basis of the fossil material. Much of the bone microarchitecture is well preserved, but a thin section of compact bone from one of the affected posterior left ribs, examined under plane and polarized light microscopy, revealed apparently normal Haversian systems, lacunae, and irregular cement lines. While fusion of cervicals 2 and 3 sometimes occurs in manatees (Petit, 1928), the other symptoms seen here have not been reported in Recent sirenians; thus the disease remains unidentified.

ACKNOWLEDGEMENTS

We thank Bruce Welton for making a thin section of the sea cow rib, and the Kaiser Sand and Gravel Co., Felton, California, Cuesta College, San Luis Obispo, California, and J. E. Bowen for donation of the specimens.

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PALEOBIOS

Contributions from the University of California
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No. 19 August 30, 1975

COLLECTION OF TAPHONOMIC INFORMATION FROM FOSSIL AND RECENT VERTEBRATE SPECIMENS WITH A SELECTED BIBLIOGRAPHY

by

Kathleen Munthe and Samuel A. McLeod

COLLECTION OF TAPHONOMIC INFORMATION FROM FOSSIL AND RECENT VERTEBRATE SPECIMENS WITH A SELECTED BIBLIOGRAPHY

BY

KATHLEEN MUNTHE[1] AND SAMUEL A. McLEOD[1]

INTRODUCTION

Paleoecology, the study of the relationships between fossil species and their environments, encompasses the events occurring between the birth and death of individuals. A goal of paleoecology is to derive information from a fossil assemblage about the biotic communities which it represents and how these communities change through time. The first step in the paleoecological interpretation of a fossil assemblage is the determination of whether the assemblage represents a biocoenose (life assemblage) or a thanatocoenose (death assemblage). If the latter, the community or communities represented by the thanatocoenose must be recognized.

In his approach to the problem of thanatocoenoses, Shotwell (1955) assumed that vertebrates most often died and were buried in or near their preferred habitats. He devised a method, based on completeness of preservation and relative density of species, for separating proximal and more distant communities from a fossil assemblage. Shotwell later applied his method to a variety of Pliocene faunas (1958, 1963).

Shotwell's methods have been criticized by Wilson (1960) and Voorhies (1969). Some of these criticisms have been aimed at Shotwell's idea that the dominant factor affecting completeness of preservation of fossil species is distance of transport from the site of origin. He failed to look closely at other events occurring after the death of individuals. These events fall within the realm of taphonomy.

The term taphonomy was first used by Efremov (1940, p. 85) for "the study of the transition (in all its details) of animal remains from the biosphere to the lithosphere". Events within this transition, some of which have been summarized and discussed by Behrensmeyer (1975), include cause of death, decomposition and disarticulation, weathering, transport, hydrodynamic sorting, burial and diagenesis. All these factors have a bearing on the differential preservation of organic remains.

Taphonomic, as well as geologic, biologic and geochemical evidence can provide a strong basis on which to make paleoecological interpretations. Fossil sites should, therefore, be collected with the purpose of gathering taphonomic histories, as well as

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specimens. Among vertebrate workers, there has been little extensive collection and utilization of taphonomic data. Exceptions include Voorhies (1969) and Behrensmeyer (1975) who drew paleoecological conclusions based on taphonomic and other evidence. In addition, the theoretical and experimental work of these authors provides a greater understanding of bones as sedimentary particles.

Although these and other vertebrate workers have gathered and utilized varying amounts of taphonomic information there is, at present, no comprehensive source of data or references for taphonomic research. It is the purpose of this paper to provide checklists for obtaining taphonomic information from both fossil and Recent vertebrate specimens. These lists contain items which bear on the conditions under which fossils are formed and accumulate. It is important that as much taphonomic information as possible be gathered during fieldwork at a fossil site, even if the collector is not directly interested in its application. Some of this information, once lost, cannot be recovered. There is also a need for data from Recent specimens. Vertebrate fossils vary in state of preservation from articulated skeletons to isolated fragments. Observation of Recent skeletons undergoing taphonomic processes shows many analogues to fossil occurrences and provides a basis for their interpretation.

It is hoped that these checklists will serve as a guide to the collection of such data. If there is a common basis for data collection, this should help to accelerate a more general understanding and appreciation of taphonomy in vertebrate paleontology. The results of such data collection can later be compiled to serve as a foundation for more refined taphonomic studies. Thought should be given to the establishment of a central location for the storage of such data.

The selected, annotated bibliography contains references chosen to introduce the reader to literature pertinent to taphonomic studies. The reader is also referred to the bibliographies in the papers by Voorhies (1969), Gradzinski (1969) and Behrensmeyer (1975).

We would like to thank A. K. Behrensmeyer, J. T. Gregory, and J. Munthe who reviewed this paper and offered many useful comments and criticisms. Special thanks are due to A. K. Behrensmeyer and D. Gifford for their contributions to the field data sheets included with this paper.

TAPHONOMIC CHECKLIST FOR RECENT VERTEBRATES

Locality

1. Date(s) of observation.
2. Map reference and specific loaclity information.
3. Locality photographs--with scale, directions, clarifying

comments.

4. General annual climate--range of temperature, humidity, precipitation.
5. Weather at time of, and between, observations.
6. Daily exposure of specimen to sun.
7. General topography.
8. Substrate--type, moisture content, organic content and its degree of decay, angle of slope upon which specimen rests.
9. Degree and agent of burial of specimen.
10. Proximity of specimen to actual or potential water source--type of source, vertical and horizontal distance to specimen, relationship of specimen to high water marks.
11. Characteristics of water source--general dimensions, relative current velocity, etc.
12. Probability of specimen or element transport by water source or other agent within a year.

Biotic Factors

1. Vegetation--type, density, proximity to specimen.
2. Predators or scavengers sighted.
3. Parts of specimen eaten by predators or scavengers.
4. Tracks, scat, feathers, burrows, etc. in proximity of specimen.
5. Evidence of human activity.
6. Maggots, dermestids or other insects on specimen.
7. Recent fauna of area--major components including domestic animals and humans.

Specimen

1. Species identification(s).
2. Individual age(s).
3. Photos and plot of specimen--with directions, scale, clarifying comments.
4. Soft parts present, including skin, ligaments.
5. Bloating.
6. Distortion due to dehydration or mummification, including position of limbs and neck relative to rest of specimen (folded, extended, etc.).
7. Degree of disarticulation.
8. Area of scatter.
9. Elements missing, including teeth.
10. Surface features of bones:
    - Tooth checking (cross-hatch cracking on tooth surface)
    - Tooth splitting
    - Mechanical breakage or crushing
    - Fractures
    - Bone flaking or cracking
    - Bone dissolution
    - Abrasion
    - Toothmarks
    - Rootmarks
    - General state of weathering.

11. Estimated time since death.
12. Inferred cause of death.

DISCUSSION

The checklist for Recent vertebrates contains the range of information useful in the understanding of taphonomic processes. Those data which can be gathered in the field have been arranged on easily-reproducible field data sheets, included with this paper. It is realized that not all items on these sheets are applicable to all specimens, but hopefully the data sheets are flexible enough to be of use in most situations encountered in the field.

Major questions arise during consideration of the origin of fossil accumulations: What effect does mode and place of death have on the availability of skeletal elements for fossilization? What factors operate in destruction of a carcass after death? What determines the rate and extent of transport and burial of a specimen after death? What are the causes of destruction? Recent taphonomic studies can help provide answers to these questions. It will be useful to consider the types of information which can be gained from certain of the items on the checklist.

The environment in which death occurs affects the preservation potential of a specimen. A number of factors operate in destruction of a specimen after death, rate and degree of burial and transport, and destruction after burial. Climatic conditions affect rate of decay or drying of soft parts and surface deterioration of bone. Warm, humid conditions favor decay and bone dissolution; dry conditions favor mummification and cracking or splitting of bones and teeth. Climatic conditions may also affect rate and degree of transport. Precipitation contributes to downslope movement of bones, and flash floods or sheetwash may transport bones great distances and at great rates.

Topography, as it relates to drainage, establishes possible routes for dispersal. The steepness of the slope upon which the specimen rests, and the erosion potential of the substrate, will operate in the dispersal or burial of a specimen. The moisture content of the substrate will affect the rate of decay. Degree of microorganismal activity may be indicated by the degree of decay of the organic content of the soil. Soil moisture and ground water activity may leach organic materials from bone, facilitating destruction. Compaction of sediments and expansion and contraction of soil can cause distortion or breakage.

If not buried quickly after death, a specimen will, in most cases, be rapidly destroyed. We have chosen a year as the time interval in which the chance of transport outweighs the chance of destruction. If transported before destruction, there is a probability that a skeleton, or parts of it, will be preserved. Dimension, current velocity, and many characteristics of a drainage which are beyond the scope of this paper will contribute to degree and rate of transport. Proximity of the specimen to a source of water will increase the chances of transport. If death occurs in an aquatic environment, probability of preservation and/or transport is high.

A number of biotic factors have an effect on destruction and transport of skeletons. Plants stabilize soil against erosion and act as traps for both bones and soil. Such activity can, therefore, inhibit dispersal and contribute to burial of a specimen. Acids released by plant roots can etch bones, contributing to their deterioration.

Predators and scavengers, through differential consumption, have a great effect on which portions of a skeleton will be available for preservation. They are important in the initial dispersal of a skeleton and may remove elements to other environments, thus affecting where preservation will occur. Toothmarks, tracks and scat provide indirect evidence for such activity. Small scavengers, such as insects, rodents and birds, can contribute to the removal of small elements.

Taxonomic and individual age determinations, from taphonomic study of Recent specimens, may provide a greater understanding of the biases seen in the fossil record. Carcass surveys of entire drainage systems may be most important here, but information gained from single specimens or mass death situations is certainly valuable.

Characteristics of a specimen itself can impart much information regarding agents of destruction and potential for transport and burial. Degree of disarticulation and burial and area of scatter have a bearing on which elements will be preserved together. A tally of elements present and missing may provide further understanding of the preservational biases in the fossil record. Surface deterioration will affect completeness of preservation, and abrasion can indicate amount of transport which has occurred. These surface features can tell much about the taphonomic histories of bones.

Mummies, elements held together by skin or ligaments, or carcasses bloated by gases can result in associated elements being transported together for some distance and probably being deposited together. The action of individual bones as sedimentary particles involves the size, shape and density of the bones. These have been considered by Voorhies (1969) and Behrensmeyer (1975). The orientation of elements is important if transport has occurred.

Mode of death is also important in determining the availability of specimens for preservation. The role of predators and scavengers in this regard has already been discussed. Mass death situations, through drownings or other means, produce an abundance of carcasses. If there is a high prey:scavenger ratio, the probability of preservation for at least some of these carcasses is high. Such assemblages could yield valuable information and should be studied taphonomically.

Recent taphonomic studies are of value because they can shed light on which processes are likely to remove which skeletal parts and which elements are likely to be preserved together. Temporal control on observations provides information on the rate at which these processes occur in various environments. Such information is essential to our understanding of the formation of the fossil record.

TAPHONOMIC CHECKLIST FOR FOSSIL VERTEBRATES

Locality

1. Date(s) of observation.
2. Specific locality information.
3. Air photo or map reference.
4. Locality photographs--with directions, scale, clarifying comments.
5. Collecting conditions affecting access, visibility.
6. Collecting methods.
7. Collecting biases.

Geological Observations

1. Stratigraphic position.
2. General topography.
3. General geological history of the area.
4. Fossiliferous strata--number and exposure of beds, extent.
5. Lithology of fossiliferous strata:
   -Composition
   -Color
   -Sorting
   -Grain size
   -Rounding
   -Compaction
   -Depth of weathered surface.
6. Sedimentary structures.
7. Current directions.
8. Inferred depositional environment(s).
9. Sedimentary microstructure around bones.

Fossil Material

1. Type of locality--quarry, surface prospect, cave, etc.
2. Photos and plot of accumulation--with directions, scale, clarifying comments.
3. Specimen distribution--vertical, horizontal, relation to lithologic boundaries.
4. Plant and invertebrate remains.
5. Assemblage of bones--concentration, size range, proximity of

bones to one another.

6. Degree of disarticulation and tooth loss.
7. Orientations of skulls, proximal ends of long bones, or articulated skeletons.
8. Flexion or extension of body parts of articulated specimens.
9. List of elements present.
10. Surface features of bones, pre- or post-fossilization:
    -Cracks
    -Fractures
    -Crushing
    -Abrasion
    -Flaking
    -Color
    -Solution
    -Rootmarks
    -Tooth splitting
    -Tooth checking
    -Distortion
    -Toothmarks.
11. Number and proportions of taxa represented.
12. Maximum numbers of individuals.
13. Size range of animals.
14. Individual ages.
15. Possible origin for bone concentration.

DISCUSSION

The checklist for fossil vertebrates incorporates the geological and paleontological data allowing reconstruction of communities from thanatocoenoses. Those data which can be collected in the field have been arranged on field data sheets. It is hoped that these data sheets are flexible enough to be of use in most situations encountered in the field. The last page of the field data sheet may be utilized for a single specimen, many specimens of a single taxon, or for several taxa where remains are not abundant. Replication of this page may be desirable.

Except in unusual conditions, such as a volcanic ash fall, fossil sites do not usually preserve the standing population of a community. Therefore, an analysis of the fossil taxa present is alone insufficient for drawing conclusions about the communities from which the animals came. One must attempt to discern the processes which influenced the accumulation and preservation of a fossil assemblage. Most of the items on the checklist pertain to the transportation of elements to the depositional environment and the characteristics of the depositional environment. Other items deal with processes affecting the specimens before transport.

Location of the fossil site should be given in as much detail as possible to allow return to the site for additional observation or collection. Information pertaining to collecting methods and biases is important in determination of the degree to which fossil material is representative of the locality. It is difficult to discern from many paleontological publications which taxa or elements were actively sought.

The geological context of fossil accumulations is of great importance in determining the formation of those accumulations. Characteristics of the fossil-bearing sediments may indicate environment of deposition and mode and distance of transport. The microstructure of sediments directly surrounding a specimen may indicate whether the specimen itself acted as a sedimentary particle and whether decay of soft parts was completed before or after burial.

Careful examination of the specimens themselves can yield much useful information. Orientation of bones, particularly long bones, can indicate current directions, as can orientation of plant fossils and certain sedimentary features. Degree of articulation and surface features of bones can reveal much about the events occurring between death and fossilization.

Much useful taphonomic information can also be gathered in the laboratory. Taxonomic information and age determinations may help to determine the relationship of the fossil accumulation to the standing population and point to preservational biases. These data, as well as the size range and relative abundances of elements, can provide information about sorting processes.

Many of these data are routinely collected during collection and study of fossil accumulations. However, the full range of information presented here is necessary if we are to derive more accurate information from fossil assemblages about the biotic communities which they represent.

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no. 19 Appendix A

TAPHONOMIC FIELD DATA SHEET FOR FOSSIL VERTEBRATE SPECIMENS

Name____________________

Date____________________

Locality____

____

____

Air photo or map reference____

Type of fossil locality:

_____ Quarry   Other_______________________________

_____ Surface prospect   ____________________________________

_____ Washing site   _____ Single specimen

_____ Cave   _____ Many specimens

Collecting conditions affecting access, visability, etc.________________

____

____

____

Collecting methods:

_____ Prospect   Other_______________________________

_____ Quarry   ____________________________________

_____ Sieve   ____________________________________

Possible collecting biases:

Specimen size____

Taxonomic____

Completeness____

Equipment____

Number of collectors____

Training of collectors______________________________________

Estimated % of fossils collected____________________________

Other____

____

Stratigraphic position:

Formation____

Member____

Beds____

Age____

Topography____

____

____

no. 19 Appendix A

PHOTOGRAPHIC RECORD OR SKETCH
(Include scale)

TAPHONOMIC FIELD DATA SHEET FOR FOSSIL VERTEBRATE SPECIES

Name____________________

Date____________________

Fossiliferous strata:

Number of beds____________________

Exposure of beds____________________

Thickness and variation____________________

Lateral extent and variation____________________

Relation to barren strata____________________

Lithology of fossiliferous strata:

Composition____________________

Color____________________

Sorting____________________

Grain size____________________

Rounding____________________

Compaction____________________

Depth of weathered surface____________________

Other____________________

Sedimentary structures:

Cross bedding____________________

Ripple marks____________________

Mudclasts____________________

Mudcracks____________________

$CaCO_3$ nodules____________________

Tracks____________________

Burrows____________________

Rootcasts____________________

Other____________________

Additional geological observations:

Plant and invertebrate remains, preferred orientations

Current directions

Inferred depositional environment(s)

Position of specimens:

Vertical distribution

Horizontal distribution

Relation to lithologic boundaries

Sedimentary microstructure around bones:

Gaps

Color

Slumping

Impressions

Concretions

Adherence of matrix to bones

Other

no. 19 Appendix A

TAPHONOMIC FIELD DATA SHEET FOR FOSSIL VERTEBRATE SPECIMENS

Name____________________

Date____________________

Assemblage of bones:

Concentrated____________________ Dispersed____________________

Size range of bones____________________

Articulated skeletons--orientations, flexion and extension of body parts__________

____

____

____

____

Disarticulated skeletons--area of scatter, orientation of elements__________

____

____

____

Unassociated elements--concentration, preferred orientations of proximal ends of long bones____________________

____

____

____

Proximity of bones to one another____________________

____

____

Surface features of bones (check left if post-fossilization):

_____Cracks____________________

_____Fractures____________________

_____Crushing____________________

_____Abrasion____________________

_____Flaking____________________

_____Color____________________

_____Solution____________________

_____Rootmarks____________________

_____Tooth splitting____________________

_____Tooth checking____________________

Distortion____________________

Toothmarks____________________

_____Other____________________

____

____

Detailed account of specimen(s):

Taxon (Indicate left if more than one)______________________________

Elements		# Present	Comments (completeness, orientation, surface features, general state of weathering, etc.)
Skull			
Mandible	r l		
Isolated teeth			
Cervicals			
Thoracics			
Lumbars			
Sacrum			
Caudals			
Sternabrae			
Ribs			
Scapula	r l		
Humerus	r l		
Radius	r l		
Ulna	r l		
Innominate	r l		
Femur	r l		
Tibia	r l		
Fibula	r l		
Foot bones			

no. 19 Appendix B

TAPHONOMIC FIELD DATA SHEET FOR RECENT VERTEBRATE SPECIMENS

Specimen#________________

Date________________

Observer________________

Species________________

Individual age(s)________________

Map reference________________

Specific locality information________________

____

____

Weather________________

General topography________________

____

Substrate:

Type________________

Moisture content________________

Organic content________________

Degree of decay________________

Angle of slope________________

Degree and agent of burial________________

____

____

Proximity of specimen to actual or potential water source:

____ In water. If not: ____ River or stream ____ Dry wash

____ Horizontal distance ____ Pond or lake ____ Sheet wash

____ Vertical distance ____ Spring Other________________

Relationship to high water mark________________

Characteristics of water source:

General dimensions________________

Relative current velocity________________

Other________________

____

Probability of specimen or element transport by water source or other means within a year:

____

Daily exposure of specimen to sun________________

Vegetation-type, density, proximity to specimen________________

____

____

no. 19 Appendix B

PHOTOGRAPHIC RECORD OR SKETCH
(Indicate scale)

no. 19 Appendix B

TAPHONOMIC FIELD DATA SHEET FOR RECENT VERTEBRATE SPECIMENS

Specimen #__________

Date__________

Evidence of vertebrate predators or scavengers:

Sightings__________

Tracks__________

Scat__________

Hair or feathers__________

Toothmarks__________

Soft parts eaten__________

Insects associated with specimen:

Dermestids__________	Flies__________	Other__________
Maggots__________	Ants__________	__________

Other fauna:

Burrows__________

Cattle or other ungulates__________

Human activity__________

Other__________

State of specimen:

Complete__________	Disarticulated__________
Mummified__________	Bloated__________
Distorted__________	Odor__________

Soft parts present__________

Degree of disarticulation__________

Area of scatter__________

General state of weathering of bones__________

Estimated time since death__________

Inferred cause of death__________

no. 19 Appendix B

DETAILED ACCOUNT OF SPECIMEN:

		Present	Exposed from skin	Comments (completeness, breaks, surface features, etc.)
Skull				
Mandible	r			
	l			
Upper dentition	r			
	l			
Lower dentition	r			
	l			
Cervicals				
Thoracics				
Lumbars				
Sacrum				
Caudals				
Sternum				
Ribs	r			
	l			
Scapula	r			
Humerus	r			
	l			
Radius	r			
	l			
Ulna	r			
	l			
Manus	r			
	l			
Innominate	r			
	l			
Femur	r			
	l			
Tibia	r			
	l			
Fibula	r			
	l			
Pes	r			
	l			

% original bones still present ____________

Paleo Bios

Museum of Paleontology
University of California, Berkeley

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A MANDIBLE OF *BECKIA* (MAMMALIA: MUSTELIDAE) FROM CONTRA COSTA COUNTY, CALIFORNIA

BY STEPHEN W. EDWARDS[1]

ABSTRACT

A second specimen of *Beckia* Bryant, from the Mio-Pliocene undifferentiated Contra Costa Group in Contra Costa County, California, closely resembles the type of *Beckia grangerensis* Bryant. The Kendall-Mallory local fauna, which includes the specimen of *Beckia*, appears to be slightly older than the Black Hawk Ranch local fauna, and late Clarendonian in age.

INTRODUCTION

The mandible described here (UCMP 112158) is from the Kendall-Mallory locality (UCMP V6107), which is exposed by a roadcut in the undifferentiated Contra Costa Group in Bolinger Canyon, Contra Costa County, California. The lithology of the locality, which produced most of the Kendall-Mallory local fauna, is a light gray to dark olive-green fluvial siltstone and mudstone. A prominent pebble-cobble conglomerate, interbedded with brown, poorly sorted sandstone, rests conformably on the fine clastic beds, fifteen feet above the quarry.

The only previously reported specimen of *Beckia* is the holotype (LACM 10642) from Yakima County, Washington. The California specimen extends our knowledge of the paleogeographic distribution of this genus, as well as of the tribe Mellivorini, fossil remains of which are extremely rare in the Nearctic.

Abbreviations used in this paper are: LACM - Los Angeles County Museum of Natural History; and UCMP - University of California

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Museum of Paleontology.

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SYSTEMATICS

Order CARNIVORA Bowdich, 1821
Family MUSTELIDAE Swainson, 1835
Subfamily MELLIVORINAE Gill, 1872
Genus *Beckia* Bryant, 1968

Type: *Beckia grangerensis* Bryant, LACM 10642, right horizontal ramus with P_3-M_1 and roots of C to P_2, Bryant, L. J., 1968, Los Angeles County Museum Contributions in Science, number 139, figs. 1-2.

Type Locality: LACM loc. 6431, Granger Clay Pit, Yakima County, Washington; Ellensburg Formation.

Beckia cf. B. grangerensis

Figure 1

Material: UCMP 112158, UCMP locality V6107; fragment of left horizontal ramus with M_1 (broken), roots of P_{1-4}, posterior part of alveolus of C; fragment of right horizontal ramus with P_4-M_1 (both broken).

Description: The teeth are well worn. The entoconid region of M_1 is obscured by wear. A small entoconid may have been present, but if so was very reduced relative to the large hypoconid. The paraconid is longer than the talonid. There is no metaconid. There is no cingulum surrounding the hypoconid (as in the holotype), but this may be an artifact of enamel breakage and loss. P_4 is two-rooted, and shows a small posterior cingulum and a very slight posterior accessory cusp between the cingulum and the main cusp. P_{2-3} are both two-rooted. P_1 is very reduced, and single-rooted. The anterior end of P_3 is oriented labially, and labially overlaps the posterior end of P_2. P_2 shows the same orientation as P_3, but is even more oblique. The anterior root of P_2 is small, and the very reduced single root of P_1 is mesiolingual to it. The canine root, based on alveolus size, was substantial. The symphysis is not expanded. There are two mental foramina, one below the roots of P_2, the other below the posterior root of P_3.

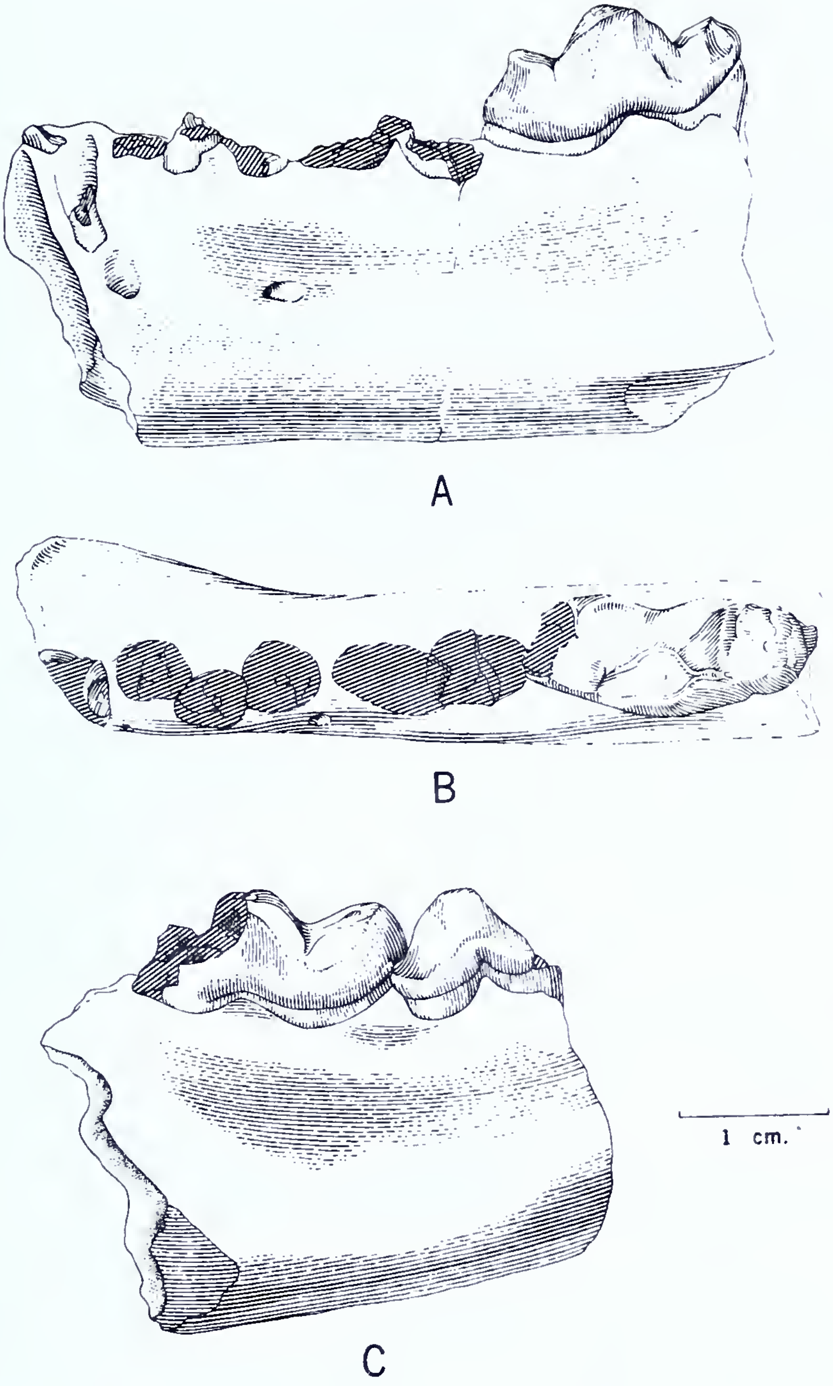

Figure 1. *Beckia cf. B. grangerensis*, UCMP 112158, loc. UCMP V6107. A. Left horizontal ramus with M_1, external view. B. Same fragment, showing P_1 root and alveoli for P_{2-4}, occlusal view. C. Fragment of right horizontal ramus, with P_4-M_1, external view.

Discussion: UCMP 112158 resembles the holotype of *Beckia grangerensis* in most details. Although the anterior mental foramen is below the roots of P_2 in UCMP 112158, and below the anterior root of P_3 in the holotype, even this character is remarkably close in the two individuals, considering how variable this feature tends to be in other mustelids (*Gulo* and *Taxidea*). However UCMP 112158 is not definitely assigned to *B. grangerensis*, because wear has made development of the M_1 entoconid region uncertain; and because the structure of the anterior premolar crowns is unknown.

Age and Correlation: The type specimen of *Beckia grangerensis* Bryant is from LACM loc. 6431, in "the upper or Naches Member of the Ellensburg Formation...above the Wenas Basalt" (Bryant, 1968, p. 3). Bryant (*op. cit.*, p. 3) reports *Hipparion ?anthonyi* from the same locality. Several well-worn cheek teeth of *Nannippus aff. tehonensis* were found at UCMP V6367, below the Wenas Basalt. This indicates the holotype of *Beckia* may be of late Clarendonian age. Hemphillian age is also a possibility, suggested by *Hipparion ?anthonyi*, which was recorded by Merriam *et al.* (1925, p. 80) from the Hemphillian Rattlesnake beds.

The mandible described in this report was collected at UCMP V6107, in association with the following mammalian taxa:

- Sciuridae
    - *?Protospermophilus sp.*
- Canidae
    - *Aelurodon aff. haydeni*
    - *Osteoborus cf. diabloensis*
- Gomphotheriidae
    - *Gen. et sp. indet.*
- Equidae
    - *Nannippus cf. tehonensis*
- Merycoidodontidae
    - *Ustatochoerus profectus*
- Camelidae
    - *Gen. et sp. indet.*

UCMP V6107 is situated about three miles west of the Black Hawk Ranch quarry (UCMP V3310). Both localities are in continental rocks overlying the marine "Neroly" Formation (*sensu* Webb and Woodburne, 1964, p. 71). The Black Hawk Ranch quarry lies approximately 1,900 feet stratigraphically above a local *Astrodapsis tumidus* zone in the Neroly. UCMP V6107 lies approximately 1,800 feet above an *Astrodapsis tumidus* bed in the Neroly of Las Trampas Ridge (flanking Bolinger Canyon). Neither *Nannippus cf. tehonensis* nor *Ustatochoerus profectus*, both recovered at V6107, have been found in the Black Hawk Ranch quarry. However, the Black Hawk Ranch quarry occurs about 300 feet upsection from a locality (UCMP V5509) which has produced *N. cf. tehonensis* teeth virtually identical to those from V6107 in Bolinger Canyon. Juvenile *Ustatochoerus* specimens from V3310 appear to fall within the size-range of *U. major*, which is larger than *U. profectus*, and later in age in the Great Plains. The Kendall-Mallory local fauna appears to be slightly older than the Black Hawk Ranch local fauna.

Nannippus cf. tehonensis teeth, much like teeth from V6107, occur near the middle of the type Grizzly Peak Formation (UCMP V1001), the base of which has been potassium/argon dated at 9.8-10.0 million years (Dr. Garniss H. Curtis, oral commun.). *Ustatochoerus profectus* has been found in the lower Ricardo Formation. The lower Ricardo (in part) has been dated at 10.0 million years (Evernden *et al.*, 1964, KA 453). On the basis of these dates, UCMP V6107 would be considered late Clarendonian in the sense of Evernden *et al.* (1974, p. 164), and either late Clarendonian or early Hemphillian in the sense of Berggren and Van Couvering (1974, fig. 11). This would clearly be older than the Ellensburg Formation locality which produced the *Beckia* holotype, if *Hipparion ?anthonyi* from that locality indicates proximity in age to the Rattlesnake fauna.

MEASUREMENTS

	UCMP 112158	LACM 10642 TYPE
P_3 antero-posterior diameter	9.4 (alveoli)	10.1
P_4 antero-posterior diameter	12.7 (alveoli)	12.9
P_4 transverse diameter	5.7	6.34
M_1 antero-posterior diameter	19.8	19.4
M_1 transverse diameter	7.3	8.3
P_1-M_1 length	51.5	- -
Depth of mandible below mid M_1	23.3	19.65

Holotype measurements are from Bryant, 1968, p. 6.

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AN INVESTIGATION OF INDIVIDUAL GROWTH AND POSSIBLE AGE RELATIONSHIPS IN A POPULATION OF *PROTOTHACA STAMINEA* (MOLLUSCA: PELECYPODA)

BY

ANNALISA BERTA[1]

ABSTRACT

Examination of various quantitative approaches to the determination of molluscan shell growth suggests that the bivalve shell is potentially valuable as a tool for the chronological recording of environmental events.

The present study employs several methods for the determination of molluscan shell growth and utilizes such data to compare growth and age characteristics for a collected population sample of little neck clams--*Protothaca staminea*. The validity of the assumption, implicit in many investigations, that the major growth bands delimited on the exterior shell surface as concentric rings are deposited in relation to an annual cycle of growth is seriously questioned. Results of the investigation suggest that until the annual nature of the external rings is demonstrated through release and recovery methods, workers attempting to use these rings to substantiate the annual periodicity of growth cycles may be misrepresenting the data and consequently under- or overestimating the ages of the populations.

INTRODUCTION

Approaches to the interpretation of molluscan growth and mortality patterns have been given extensive treatment in the literature (for example, see Barker, 1970; Craig and Hallam, 1963; Rhoads and Pannella, 1970). Most studies have attempted to provide methods of age determination to substantiate relationships between rate of growth and age among populations of various molluscan species.

Fishery investigators have long been concerned with age determin-

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ation in molluscs. Such studies have been designed to provide growth and mortality data necessary to the economic management and control of populations. In the last twenty years, paleontologists and archaeologists have become increasingly interested in obtaining such data and applying it to ecological interpretations of fossil assemblages. Methods of molluscan age determination proposed to date and discussed in this investigation may be grouped as follows: (1) size-frequency and age analysis, (2) interpretation of growth interruption lines on the exterior shell surface and as internal microscopic features, (3) shell-weight and age analysis.

The objective of this study is to test the validity of the methods used by other workers to determine absolute age in molluscs through an analysis of the growth and age characteristics of a population sample of little neck clams (*Protothaca staminea*, Conrad, 1837). Results of the application of these age determination methods for the collected sample are then compared and conclusions are drawn regarding their usefulness in paleontological and archaeological contexts.

POPULATION SAMPLE

Protothaca staminea is most commonly known as the little neck clam but it is also cited in the literature as the rock cockle, bay cockle, heart shell clam, steamer clam, ribbed carpet shell and rock venus.

One hundred and sixty paired valves obtained from 80 live little neck clams collected from Discovery Bay on the Olympic Peninsula comprise the population sample (Fig. 1). The sample was collected during a low tide on the evening of October 11, 1973.

The shell of *Protothaca staminea* is inflated, oval to round in shape and medium-sized, reaching 66 mm in length. The external surfaces of the valves have numerous crowded radiating striae and finer concentric lines most distinct on the anterior side. The umboes and lunules are prominent and are near the anterior end of the shell. The Discovery Bay specimens are white in color with geometric patterns of wavy brown lines or blotches.

The collected specimens of *Protothaca staminea* are inhabitants of Ricketts' and Calvin's (1968) Rocky Shores Zone--Low Tide Horizon and were concentrated in coarse, silty sand along the beach.

METHODS AND MATERIALS

Linear measurements were recorded for each of the 160 valves of the Discovery Bay population of *Protothaca staminea*. Two indices of shell length were measured to the nearest 0.1 mm using dial calipers. Length_1 is the greatest antero-posterior dimension and length_2 is the transverse length of the shell measured from the umbo to a point on the posterior shell edge. These shell measurements have been standardized in the manner shown in Fig. 2. Each valve was weighed to the nearest 0.1 g using a triple beam balance.

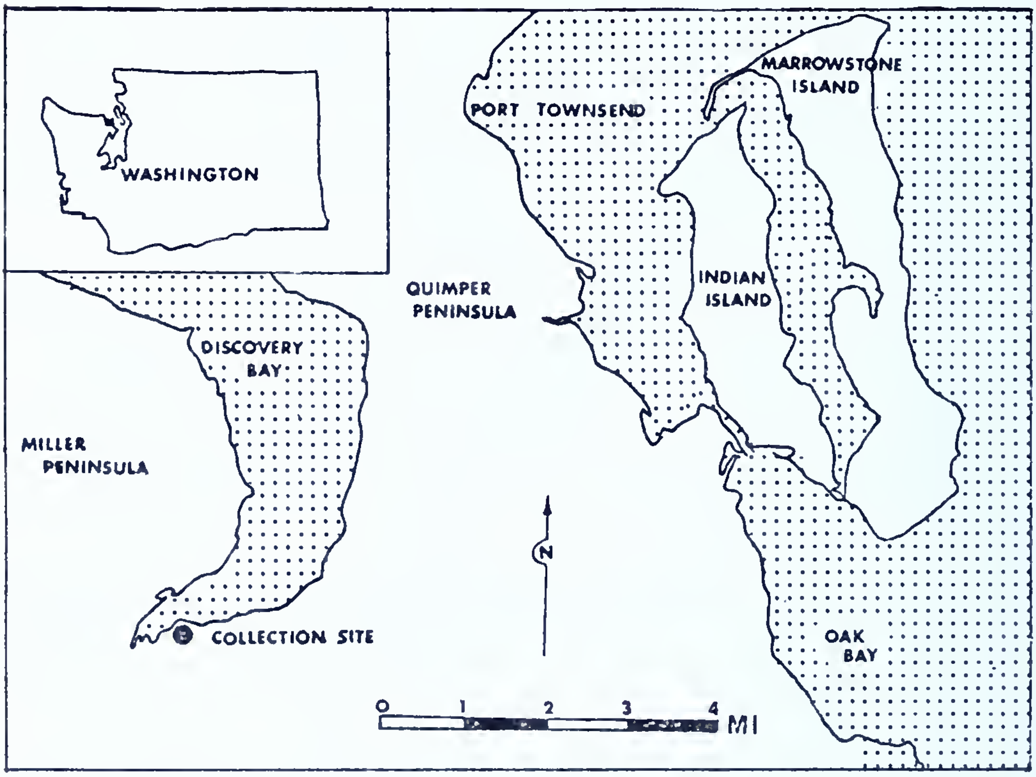


Fig. 1 Location map, Discovery Bay population of *Protothaca staminea*, Olympic Peninsula, Washington.

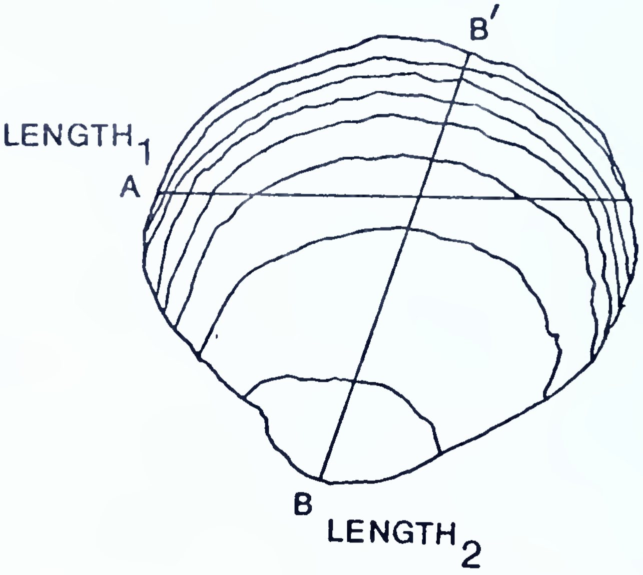


Fig. 2 *Protothaca staminea*--standardized linear shell measurements.

The ages of 20 individuals selected from the population were determined in the following manner. The major growth rings on the shell surface of *Protothaca staminea*, defined as thin concentric raised rings between larger depressed growth bands were counted as annual increments based on Barker's (1970) documentation of annual growth cycles in this species (Plate 1). Next, the microscopic increments within the shell were studied by means of thin sections. The shells were first coated with polyester resin to avoid fracture during sectioning. The plane of the transverse section passed from the umbo to the posterior shell edge along the vector of maximum growth (length_2). The cut shell surface was then polished sequentially with 45 and 15 micron diamond laps. The polished surface was epoxied to a frosted glass slide and further cut and polished to obtain a uniform thickness of shell. Subsequently, the thin section was examined under a light microscope at magnifications up to 400x and the microscopic growth increments were counted.

SIZE-FREQUENCY ANALYSIS

The size-frequency method of molluscan age determination has been much used in fishery investigations (Fraser and Smith, 1928; Quale, 1943; Weymouth *et al.*, 1925, 1931). It is based on the assumption that the ages at death of bivalves will be clearly reflected in the dimensions of the dead shells. This method has the principal advantage of enabling the investigator to estimate the age composition of the population directly from the measurement of shells in his catch without further analysis. There are, however, several difficulties in this method: (1) In the absence of other information, the ages of the youngest year class is unknown, (2) the complete absence of a year class or its poor representation in the population may lead to error in the estimated ages, (3) overlap in the size ranges of individuals at various ages due to growth in differing local environmental conditions may lead to misrepresentation of the age structure of the population. In addition, review of studies using this method of age determination reveals inconsistencies in the criteria for the linear dimensions measured.

A size-frequency histogram was constructed for the Discovery Bay population using measurements obtained from the left valves of the specimens. Size is here defined as length_1. A size-frequency plot of the sample tends to exhibit a slightly left-skewed distribution, the dispersion being greater among the smaller-sized individuals (Fig. 3). In order to deduce more from the histogram, further information is required on the growth of little neck clams.

In a size-frequency analysis by Quale (1943), who followed the growth of marked specimens of *P. staminea*, individuals of the same year class were found to vary between 1 and 10 mm at the end of their first winter. In the following summer the range of variation was found to be even greater because of the differential growth rates of the specimens. According to Quale, the growth of *P. staminea* is relatively slow; at the end of their second year, when about half the animals spawn, the average length is only 25 mm and when the balance spawn a year later the size increases to only 35 mm.

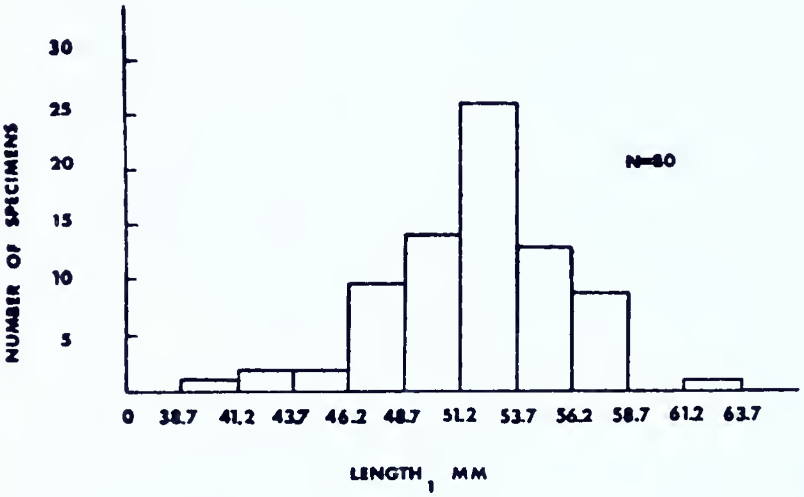


Fig. 3 Size-frequency histogram of left valves of *Protothaca staminea*.

Fraser and Smith (1928) made extensive population studies of live *Protothaca staminea* from the beaches of Vancouver Island, British Columbia. They found that populations of *P. staminea* which are protected from currents and waves tended to include a relatively large crop of juvenile and young adult individuals. In more exposed localities the population contained relatively fewer young individuals whose growth was slow in their earlier years but who grew more rapidly in their later years. Fraser and Smith further suggest that such exposed places may have a greater food supply but that the young have trouble establishing themselves because of the vigorous wave and current action. With growth, the larger clams are able to migrate to places with better food supplies. A similar reason may explain the poor representation of the smaller-sized individuals in the Discovery Bay population and the predominance of larger individuals.

If size were related to age by a linear function, one could construct a survivorship curve for the Discovery Bay population from a size-frequency diagram by using size classes as age classes. However, the studies of many investigators (Mason, 1957; Orton, 1926; Weymouth and McMillan, 1931) indicate that growth in bivalve molluscs in terms of shell length is not linear but close to logarithmic and often reflects a decrease in rate of growth of shell length with an increase in age. If one considers that the shape of a size-frequency curve is affected by the differential rates of growth of individuals it is conceivable that using size classes as age classes might result in the lumping of older individuals with younger individuals since there is no *a priori* way of recognizing the discreetness of the classes. It is suggested then that size-frequency in the absence of information linking rate of growth and size with age adds little to an analysis of population structure.

EXTERNAL GROWTH RING ANALYSIS

A more common approach to molluscan age determination involves the use of growth interruption lines, commonly termed "rings" on the exterior shell surface. These are generally interpreted as annual increments of shell growth. The "annual ring" method of age determination for molluscs was first examined by Weymouth *et al.* (1925) for *Siliqua patula* and Fraser and Smith (1928) for *Paphia* (= *Protothaca*) *staminea* and *Saxidomus giganteus*. The most comprehensive study yet undertaken (Barker, 1970) examines in detail the morphology of annual and sub-annual growth lines in shells of different species and the manner in which these features originate during shell growth, relating the processes of growth to the environment of the species. In recent years, studies by various paleontologists (Berry and Barker, 1968; Craig and Hallam, 1963; Pannella *et al.*, 1968; Rhoads and Pannella, 1970) have attempted to examine recent shell growth and to suggest the interpretation of growth lines in fossil shells. The data has been used to estimate population growth, mortality patterns and to estimate the length of the month and year in the geologic past. The "annual ring" method of molluscan age determination has been suggested by archaeologists (Coutts, 1970; Coutts and Higham, 1971; Weide, 1969) for solving problems involving the chronological dating of occupation sites.

A description of the process of shell growth and the formation of the interruption lines on the exterior shell surface is important to an evaluation of this method. One of the earliest attempts to describe shell growth was undertaken by Weymouth (1923) and substantiated by later workers, notably Barker (1970), Clark (1974), and Kennish and Olsson (1975). The molluscan shell grows by addition to its margin and inner surface. An expanded position of the mantle is most favorable to shell secretion, but physiological and environmental changes alter the rate of secretion and cause the mantle of the shell to retract. Shell growth at the margin of the valve is discontinuous, being interrupted by each complete closing of the shell. The reextended mantle reaches its previous position quite accurately but there is always some slight variation of extension leading to differences, according to Weymouth (1923:40) in the form of "visible lines on the outer shell surface."

The temporal rhythmicity of growth lines on shells has been much discussed and debated in the literature. The "annual ring" method described by Weymouth (1923) is based on the principle that yearly rings are formed as the result of the alternations of rapid and slow rates of growth, which are dependent on environmental events, for example, seasonal change. More recent studies (Barker, 1970; Pannella and MacClintock, 1968; Rhoads and Pannella, 1970) have revealed that these annual cycles of growth seem to be controlled primarily by temperature and therefore reflect this environmental factor.

There is, however, disagreement as to the means of differentiating between rings which indicate temporal rhythmicity and "disturbance rings" which are caused by a number of physiological and environmental events, including reproduction and changes in salinity. As a method of distinguishing annual rings from disturbance rings, Craig and Hallam (1963) suggest that every ring in the population samble be recorded and the most significant ring sizes selected. Ideally, this class-frequency plot of ring sizes should reflect major environmental events recorded by all members of the population. Inseparable from this problem is the initial difficulty encountered in estimating age classes directly from size classes. Shells which shown an overlap in the size ranges of individuals of different ages would be expected to reflect considerable variation in the number of external rings. The investigator who attempts to utilize a class-frequency plot to distinguish between annual rings and disturbance rings must take into account initial variability in the size of individuals as well as the relationship between size and number of external rings.

Most investigators, however, work from the assumption that the major growth bands, delimited on the exterior shell surface as concentric rings, are deposited in relation to an annual cycle of growth. For purposes of this study it was assumed that the major growth lines on the shell surface of *Protothaca staminea* were annual increments following the work of Barker (1970) on shell growth in this species.

The "annual ring" method of age determination for the Discovery Bay population was evaluated by plotting the number of concentric rings on the shell surface against specimen length_1 and length_2 (Fig. 4). Fig. 5 shows standard deviations and the means of length_1 of the specimens at each year of growth. An overlap is evident in the size ranges of individuals from one year class to the next--a factor previously discussed as a potential source of error in estimating the age composition of a population directly from size measurements. A plot of specimen length_1 against length_2 suggests a linear allometric growth relationship indicated by the tendency of the points to lie along a straight line which passes through the origin (Fig. 6). The correlations between the shell measurements are reported in terms of the product moment correlation coefficient-r (Sokal and Rohlf, 1969). The high degree of correlation between length_1 and length_2 ($r = 0.9681$) suggests that either dimension might be used to determine the age-length relationship. Of the two dimensions, however, length_2 is more closely correlated ($r = 0.8528$) with the age of the population as determined from growth ring analysis.

Assuming that the major growth rings on the exterior shell of *P. staminea* are annual, an age-frequency histogram was constructed for the Discovery Bay population using data derived from the left valves of the specimens (Fig. 7). The histogram is polymodal, the first cluster reflecting the six year through eight year class. Smaller clusters represent the ten and twelve year old individuals in each year class. Growth ring analysis suggests, then, that the Discovery Bay population ranges in age from four through thirteen years, the largest number of specimens representing individuals

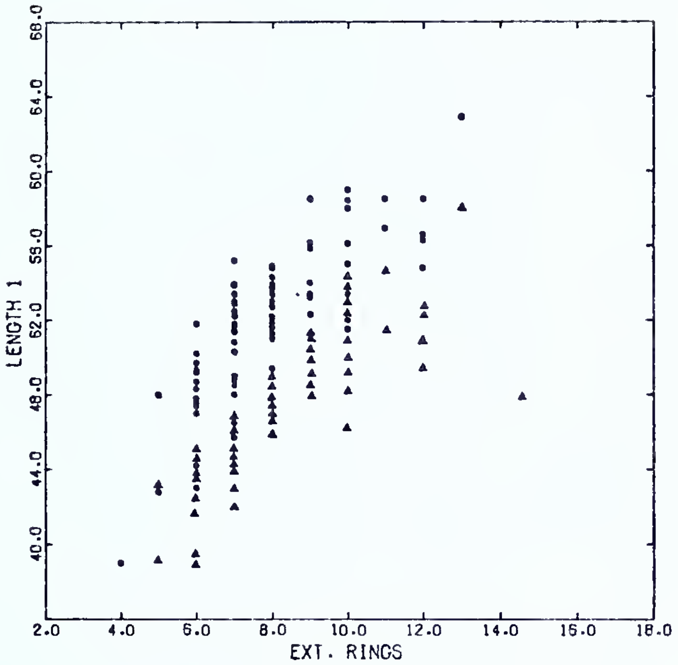


Fig. 4 Scatter diagram of shell $length_1$ (circles) and $length_2$ (triangles) in mm plotted against number of external rings and fitted by regression ($length_1$: $y = 37.567 + 1.843$; $r = 0.8146$) ($length_2$: $y = 33.027 + 1.778$; $r = 0.8528$) in *Protothaca staminea*. $n = 80$.

within the seven and eight year old classes.

Another aspect of population analysis involves the use of survivorship curves, a graphic expression of mortality rates in organisms (Deevey, 1947). The slope of the survivorship curve is proportional to the mortality rate and the change in slope along the length of the curve can be used to distinguish mortality patterns.

An attempt has been made to construct survivorship curves for the Discovery Bay population by determining the number of survivorships at each year class, using the number of growth rings on the exterior surface of the shell (Fig. 8; Table 1). The pattern of mortality for *Protothaca staminea* produces a concave curve, demonstrating a low mortality rate during the juvenile phase, increasing to a high value during youth and continuing to rise during the senescent phase of life history. The significance of this interpretation, however, clearly rests upon the validity of age determination through growth ring analysis. Precautions are necessary in the application of this method. As previously mentioned, many observers have assumed that in the various bivalve species one interruption line is added per year. It is necessary, however, to validate this assumption by supplementary observations of a given species in a particular environment before the interruption lines can be equated with annual rings.

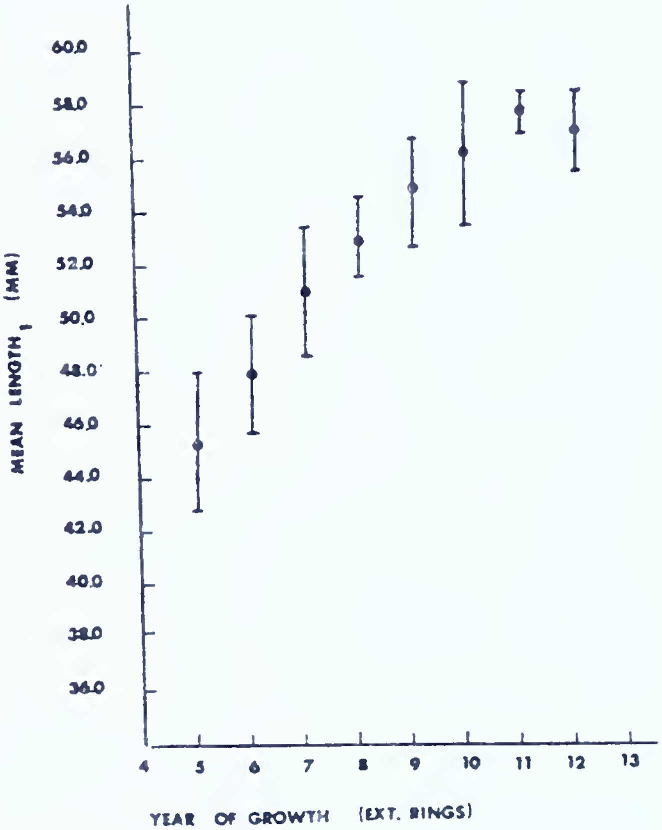


Fig. 5 Distribution of standard deviations of mean shell length$_1$ of Discovery Bay population. Vertical lines indicate one standard deviation on either side of the mean represented by solid circles.

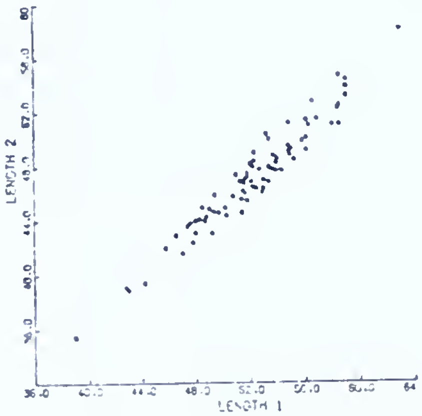


Fig. 6 Scatter diagram of shell length$_1$ in mm plotted against shell length$_2$ in mm and fitted by regression (y = .584 + .892; r = 0.9681) in *Protothaca staminea*. n = 80.

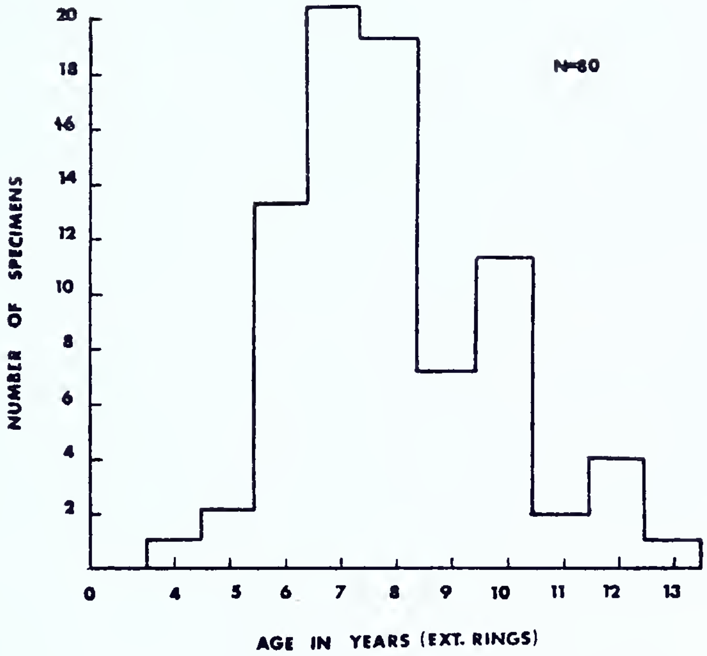


Fig. 7 Age frequency histogram of left valves of *Protothaca staminea.*

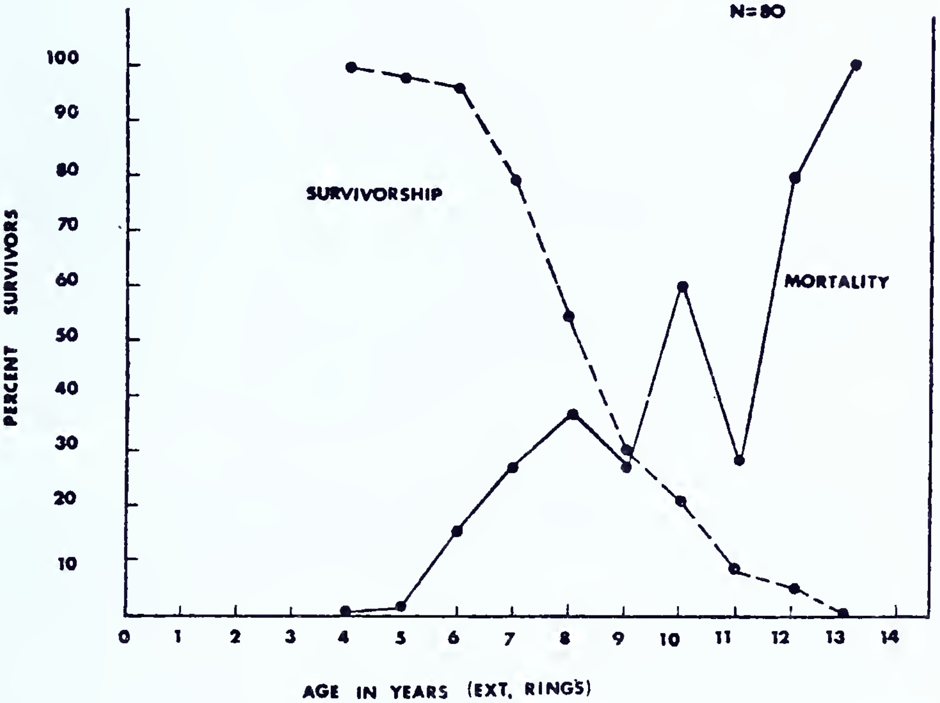


Fig. 8 Survivorship and mortality curves for *Protothaca staminea* based on data in Table 1.

Table 1. Life Table for *Protothaca staminea* based on growth rings analysis

Age Interval (years)	No. dying during age interval	No. surviving at beginning of age interval	Mortality rate as fraction of no. surviving at beginning of age interval
3-4	0	80	0
4-5	1	79	.0125
5-6	2	77	.0253
6-7	13	64	.1688
7-8	20	44	.2815
8-9	19	25	.3863
9-10	7	18	.280
10-11	11	7	.6111
11-12	2	5	.2857
12-13	4	1	.800
13-14	1	0	1.00

MICROSCOPIC GROWTH INCREMENT ANALYSIS

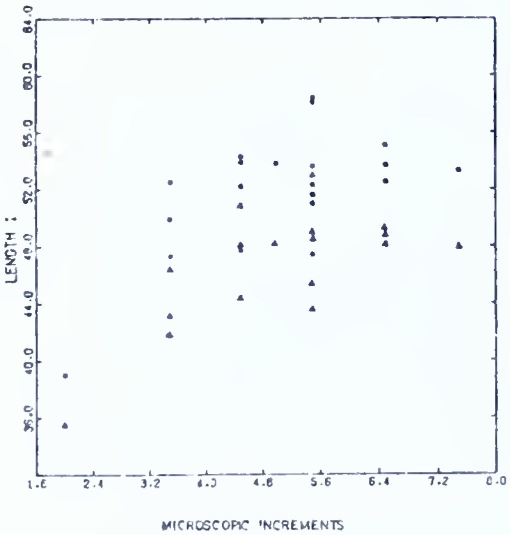
The concentric rings on the exterior shell surface of *Protothaca staminea* when viewed in thin section reveal microgrowth patterns of finer increments. These microscopic growth increments have been used as a supplementary method of molluscan age determination. The yearly, monthly, fortnightly, and daily periodicity of these increments has been experimentally demonstrated for various molluscan species (Barker, 1970; Clark, 1968; Farrow, 1971; Hall *et al.*, 1974; House and Farrow, 1968; Kennish and Olsson, 1975; Pannella and MacClintock, 1968; Rhoads and Pannella, 1970). The potential usefulness of this method in both paleontological and archaeological contexts is readily apparent, where part of the shell surface is frequently abraded or missing so as to obscure the external growth rings.

The shell structure terminology used in this microscopic analysis is adapted from Barker (1970) and Pannella and MacClintock (1968). The two major kinds of shell stratification within mollusc shells are shell layers and growth layers. The typical bivalve shell is composed of four principal calcareous shell layers and a thin covering of periostracum. The endostracum is the innermost calcareous layer secreted by the mantle. Deposits of the pallial line and adductor muscles comprise a second principal layer termed the myostracum. The two outermost calcareous layers together form the palliostracum secreted by the outer mantle fold. The innermost component of the palliostracum is secreted just outside the pallial line and is termed the mesectostracum. The outermost component is secreted by a more distal part of the mantle and is termed the ectostracum. A growth layer is here defined as one thickness of shell material deposited in a certain period of time under certain physiochemical conditions. The microscopic resolution of these growth layers is influenced by the crystalline elements of the shell structure. Barker (1964), in his microscopic analysis of the structural composition of pelecypod shells, reported a hierarchy of five cyclical groupings of growth layers. He demonstrated that these layers reflect environmental periodicities of annual and sub-annual duration.

In this study, the first order layer, characterized by a thickening and thinning of calcium carbonate and conchiolin, expressed in the mesectostracum and endostracum portion of the shell of *Protothaca staminea* by alternation of light and dark bands, is assumed to be related to an annual cycle of deposition and was selected for further examination. Microscopic observation of specimens of *P. staminea* reveal that the concentric rings on the exterior shell surface rest upon translucent, dark bands, approximately 0.4 mm in thickness. The larger depressed growth surfaces between the rings are internally defined as opaque, bright bands approximately 0.2 mm in thickness (Plate 2). Barker (1970) has demonstrated that for *P. staminea* and other bivalve species large growth increments (fast growth layers) form during the summer and narrow increments (slow growth layers) form during the winter.

The interpretation of microscopic growth increments as a method of age determination for the Discovery Bay population was evaluated in a size-frequency plot of the number of microscopic increments against specimen length$_1$ and length$_2$ (Fig. 9). Length$_2$ is most closely correlated ($r = 0.7024$) with the age of the population as determined from microscopic growth increment analysis. Standard deviations about the mean length$_2$ of the specimens at each year of growth (Fig. 10) suggest considerable overlap in the size ranges of the individuals from one class to another. No correlation was found between external growth rings and microscopic growth increments (Fig. 11). The results are not surprising, however, if one considers the lack of criteria for distinguishing annual growth rings from disturbance rings.

However, some progress toward resolution of this problem has recently been made. The work of Kennish and Olsson (1975) on shell growth in *Mercenaria mercenaria* provides definitive criteria for the recognition of different microstructural growth patterns in this species. They describe the following types of shell "breaks" or interruptions in daily shell deposition: (1) summer ("heat-shock") and winter ("freeze-shock") breaks, (2) tidal breaks, and (3) disturbance ("thermal-shock", spawning, storm) breaks and they identify each break by its corresponding growth pattern. Such information needs to be compiled for other bivalve species before one can reliably use these criteria in the interpretation of both external and microscopic shell growth patterns.



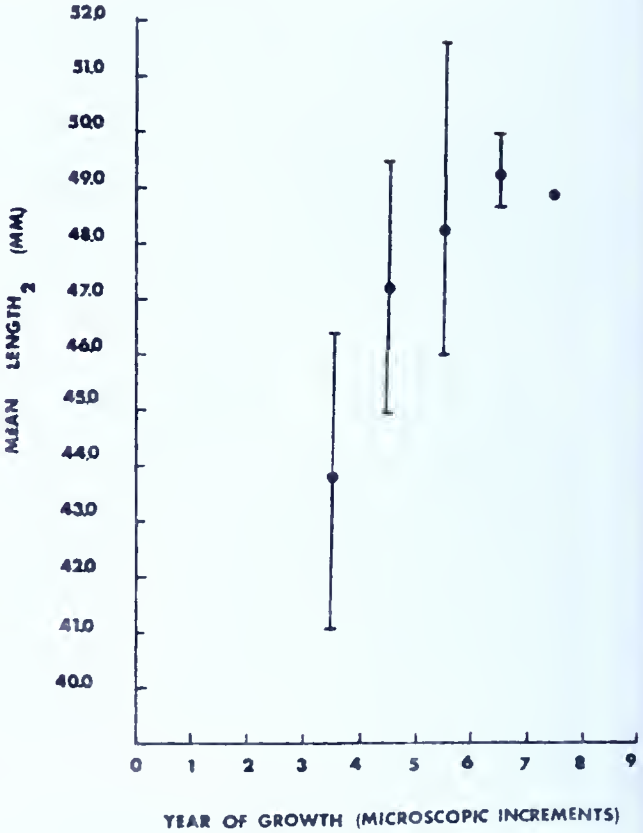


Fig. 9 (Left) Scatter diagram of shell length_1 (circles) and length_2 (triangles) in mm plotted against number of microscopic increments and fitted by regression (length_1: $y = 3.236 + 5.623$; $r = 0.7787$) (length_2: $y = 1.982 + 5.185$; $r = 0.7024$) in *Protothaca staminea.* n = 20.

Fig. 10 (Right) Distribution of standard deviations of mean shell length_2 of Discovery Bay population. Vertical lines indicate one standard deviation on either side of the mean represented by solid circles.

Determination of the age revealed by counting these rapid and slow growth layers (each couplet being counted as an annual increment) was examined in an age-frequency analysis. The age-frequency histogram (Fig. 12) for selected specimens within the Discovery Bay sample reveals a population ranging in age from 2.0 years to 7.5 years, the majority of specimens falling within the 4.5 to 5.5 year class. Disparity in the resultant ages of the population specimens is indicated by a comparison of the age-frequency histograms constructed for both the external rings and microscopic growth increments (Fig. 7 and 12).

Survivorship curves were also constructed for the Discovery Bay population from the number of microscopic increments (Fig. 13; Table 2). Comparison of the two survivorship curves (Fig. 8 and 13) indicates a similar pattern of mortality steadily increasing with age,

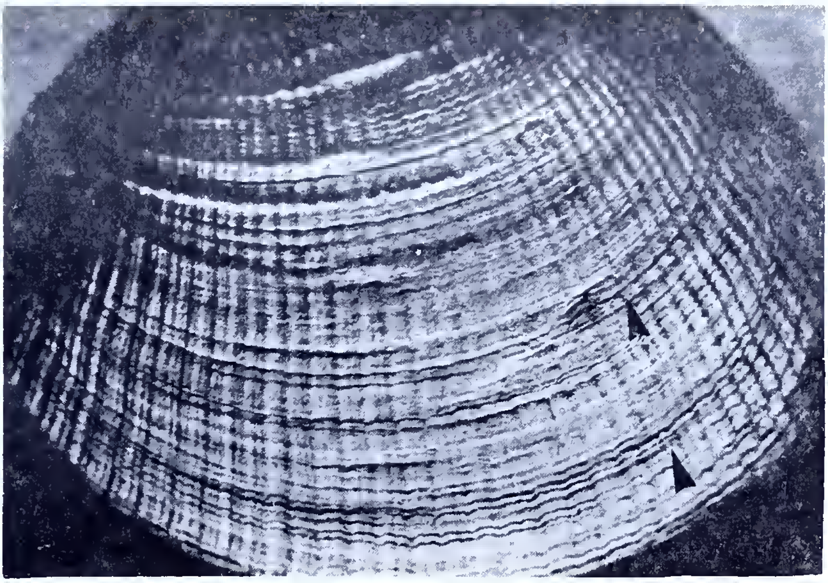
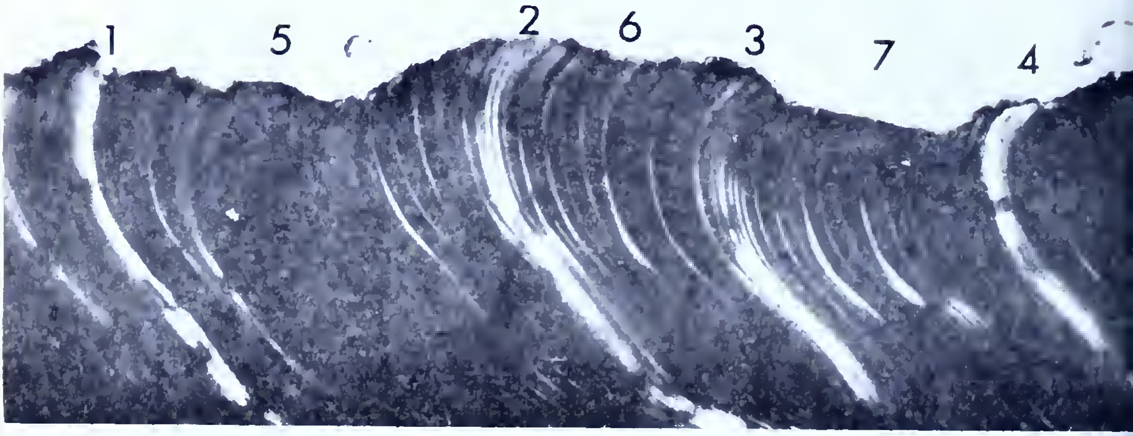


Plate 1 (Above) External growth rings of *Protothaca staminea*. Arrows indicate the major growth lines on the shell surface defined as thin concentric rings between larger depressed growth bands. These external rings were assumed to represent annual increments. X2.

Plate 2 (Facing Page) Internal microscopic growth increments in *Protothaca staminea*.

a. Transverse thin section photomicrograph illustrating alternating rapid and slow growth layers. (UCMP Hypotype 14251). Nos. 1, 2, 3, 4 indicate slow growth layers. Nos. 5, 6, 7 indicate rapid growth layers. 46X.

b. Photomicrograph illustrating the numerous microscopic increments within a slow growth layer. Such microscopic increments have been interpreted as having daily, monthly, and fortnightly periodicity. (UCMP Hypotype 14252). 58X.



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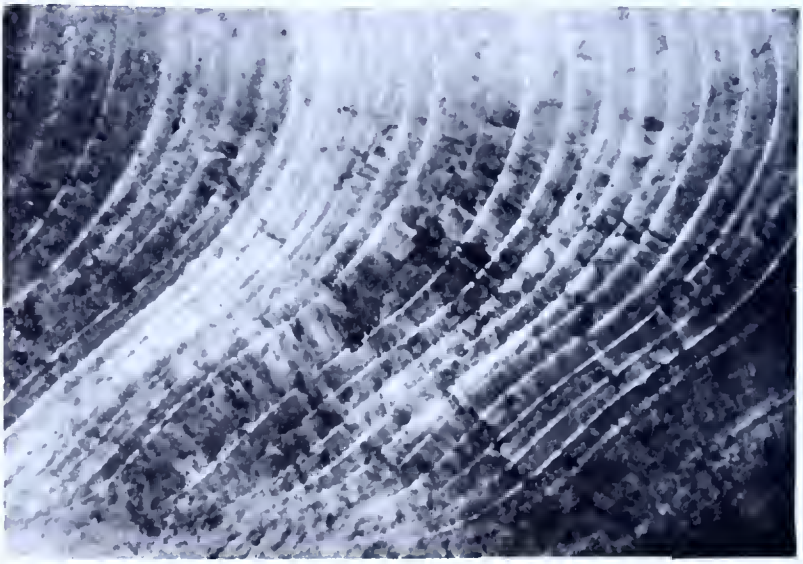

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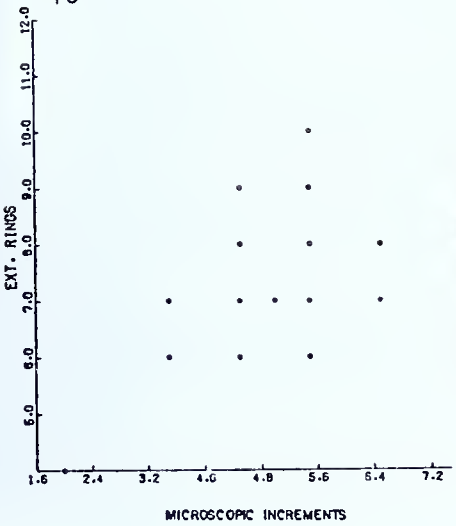


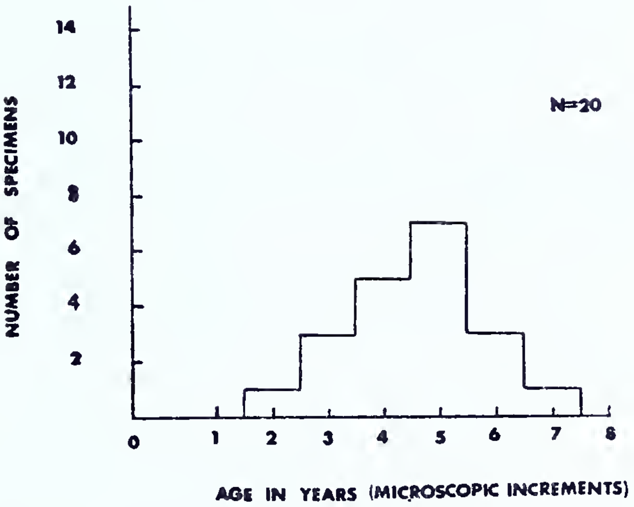


Fig. 11 (Left) Relationship between external rings and microscopic increments.

Fig. 12 (Right) Age frequency histograms of right and left valves of *Protothaca staminea*.

Table 2. Life Tables for *Protothaca staminea* based on microscope increment analysis

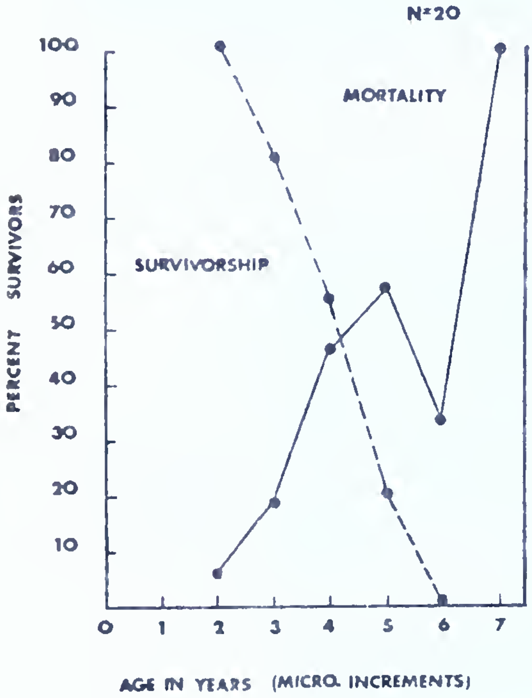
Age Interval (years)	No. dying during age interval	No. surviving at beginning of age interval	Mortality rate as fraction of no. surviving at beginning of age interval
1-2	0	20	0
2-3	1	19	.052
3-4	3	16	.187
4-5	5	11	.454
5-6	7	4	.571
6-7	3	1	.333
7-8	1	0	1.00

the only difference between the curves being the placement of the year classes.

SHELL-WEIGHT ANALYSIS

The final method of molluscan age determination considered here is shell-weight analysis. Determination of age by means of shell weight has been proposed by several fishery investigators (Haskin, 1954; Sheldon, 1967). In the present analysis the objective was to define the relationship between shell weight and length and shell weight and age using both external growth rings and microscopic growth increments.

The correlations between both shell lengths (length$_1$ and length$_2$) and weight are reported in terms of the product moment correlation coefficient-r (Sokal and Rohlf, 1969) in Fig. 14. The higher degree



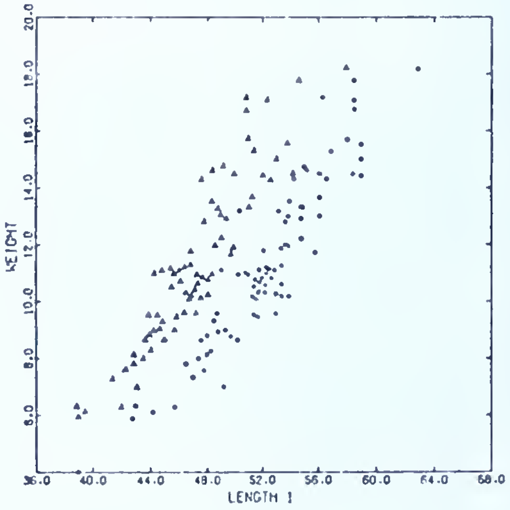


Fig. 13 (Left) Survivorship and mortality curves for *Protothaca staminea* based on data in Table 2.

Fig. 14 (Right) Scatter diagram of shell length$_1$ (circles) and length$_2$ (triangles) in mm plotted against weight in g and fitted by regression (length$_1$: y = 23.341 + .662; r = 0.9135) (length$_2$: y = 22.264 + .710; r = 0.9227) in *Protothaca staminea*. n = 80.

of correlation between length$_2$ and weight (r = 0.9227) suggests further analysis of this relationship. The relationship between shell length$_2$ and weight can be expressed by the allometric growth equation $W = aL^3$. Fig. 15 is the log-log plot of length$_2$ and weight showing the expected linear relationship.

Having demonstrated the allometry of growth for shell length and weight, the next step is to examine the relationship of shell weight and age of the population using both external growth rings analysis and microscopic increment analysis (Figs. 16 and 17). The shell weight-age relationship in both cases was quantified by linear regression equation:

$$Y = a_y + b_{yx}X$$

Utilizing the external growth rings, the slope, b_{yx} is the shell growth rate in grams/year and is plotted along with standard deviations of mean weight at each year of growth (Fig. 18). The overlap in the weight measurements of the specimens from one year class to the next indicates that the weight of individual specimens is not by itself a conclusive method of age determination.

The linear regression analysis was repeated to determine the shell weight-age relationship using microscopic growth increments. The shell growth rate is plotted along with standard deviations of mean weight at each year of growth (Fig. 19). The large deviation about the mean values suggest similarly that the weight of individual specimens using microscopic growth increments is not conclusive in the absence of other information.

DISCUSSION AND SUMMARY

In summary, examination of proposed methods of molluscan age determination by: (1) size-frequency and age group analysis; (2) growth ring analysis; and (3) shell weight and age analysis, were employed in the evaluation of growth and age characteristics of a population sample of little neck clams, *Protothaca staminea*.

The basic premise, seriously questioned here, is the validity of interpreting growth rings on the exterior of the shell as annual increments of shell addition. External and microscopic growth ring examination reveals inconsistencies in the resultant ages of the individuals. No previous attempt to compare the apparent molluscan ages indicated by these two methods has been published. Rather, investigators have become more interested in examining the finer increments of shell secretion, suggesting monthly, fortnightly, and daily patterns of growth. Substantiation of these subannual patterns of growth has been experimentally demonstrated for certain bivalve species under specific environmental conditions (Barker, 1970; Farrow, 1971; Hall *et al.*, 1974; House and Farrow, 1968; Kennish and Olsson, 1975; Pannella and MacClintock, 1968; Rhoads and Pannella, 1970). Numerical relationships between these subannual patterns of growth has suggested to a number of paleontologists variations in the length of the month and year in the geologic past

(Barker, 1970; Berry and Barker, 1968; Pannella *et al.*, 1968; Runcorn, 1968). Unfortunately, considerably less attention has been paid to the demonstration of the annual synchroneity of these external and internal increments with the environment using data derived from recent molluscan populations. Such a demonstration is clearly necessary before one can attempt to evaluate and interpret subannual patterns of growth among fossil specimens.

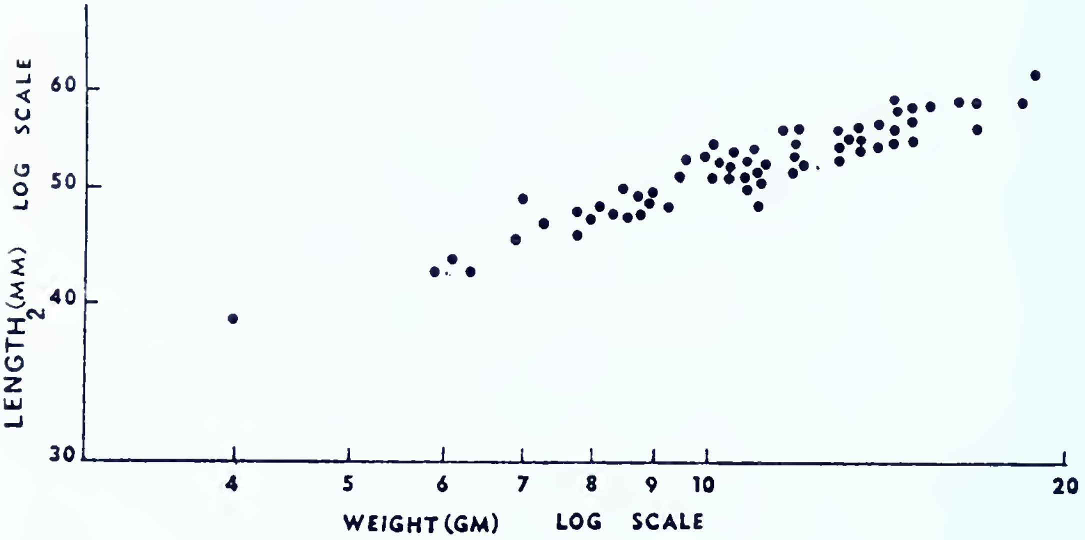
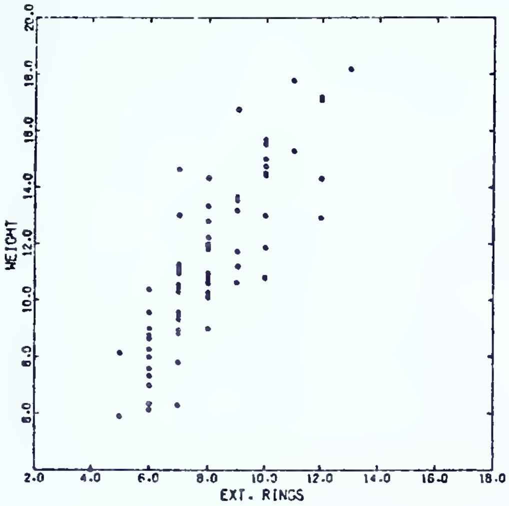


Fig. 15 Logarithmic transformation of shell $length_2$ versus weight in *Protothaca staminea*. n = 80.

As previously mentioned, this kind of analysis was not possible for the Discovery Bay population. However, there are several possible explanations for the disparity in the age structure of the population suggested by these two methods. Review of the literature reveals insufficient definition and description of these external growth rings assumed to represent annual cycles of deposition. Many workers have found it difficult to distinguish annual rings from disturbance rings. A plot of the class-frequency of all rings suggested by Craig and Hallam (1963) as a means of distinguishing annual rings is not sufficient since it selects from a size frequency distribution of ring length the most significant rings, working from the assumption that the numerical relationships of these size ranges reflect annual periodicity and not merely short-term disturbances. Rhoads and Pannella (1970), in their investigation of the growth of the clam *Mercenaria mercenaria*, demonstrated that annual rings may be distinguished by microscopic examination from disturbance rings specifically caused by spawning. In *Mercenaria mercenaria* annual breaks are characterized by an abrupt depositional break, unlike spawning breaks which are abrupt, but are followed by slow growth recovery. Kennish and Olsson (1975) provide additional criteria for the recognition of interruptions in daily shell deposition for this species. This kind of morphological criteria needs to be further evaluated for other kinds of disturbances,



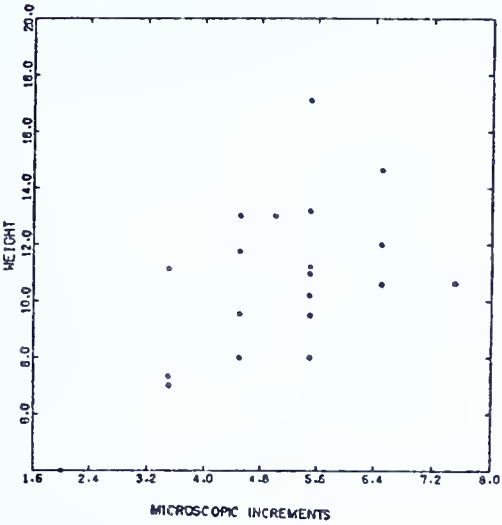


Fig. 16 (Left) Scatter diagram of shell weight in grams plotted against number of external rings and fitted by regression (y = .611 + 1.332x; r = 0.8309) in *Protothaca staminea*. n = 80.

Fig. 17 (Right) Scatter diagram of shell weight in grams plotted against number of microscopic increments and fitted by regression (y = 2.221 + 1.644x; r = 0.7450) in *Protothaca staminea*. n = 20.

such as salinity, temperature changes, and tidal fluctuations, which are also represented by external growth rings (Barker, 1964, 1970; Kennish and Olsson, 1975; Pannella and MacClintock, 1968).

It seems likely, then, that the inconsistency in the ages of the Discovery Bay sample of *Protothaca staminea* most probably stems from two sources: (1) sampling bias against juvenile individuals, (2) inadequate morphological criteria allowing discrimination of annual rings from disturbance rings. If one accepts this explanation, substantiated by data from the Discovery Bay population sample, then the validity of studies where external growth rings are assumed to represent annual periodicity may be seriously questioned. Fishery investigators using only external growth rings as a method of age determination may be grossly under or over estimating the individual ages. Paleontologists, suggesting temporal variations in the length of the geologic month and year, may have extended such interpreattions well beyond the limits of the data. Utilization of these external growth rings by archaeologists in the chronological dating of occupation sites suggests possible misrepresentation of the actual period of site habitation.

Analysis of the Discovery Bay population in terms of these quantitative approaches to molluscan age determination suggests that before the bivalve shell can be considered an accurate chronometer, experimental studies involving the observation of growth through the timed release and recovery of marked specimens of individual species must be first undertaken to clearly demonstrate the periodicity of shell rings and increments.

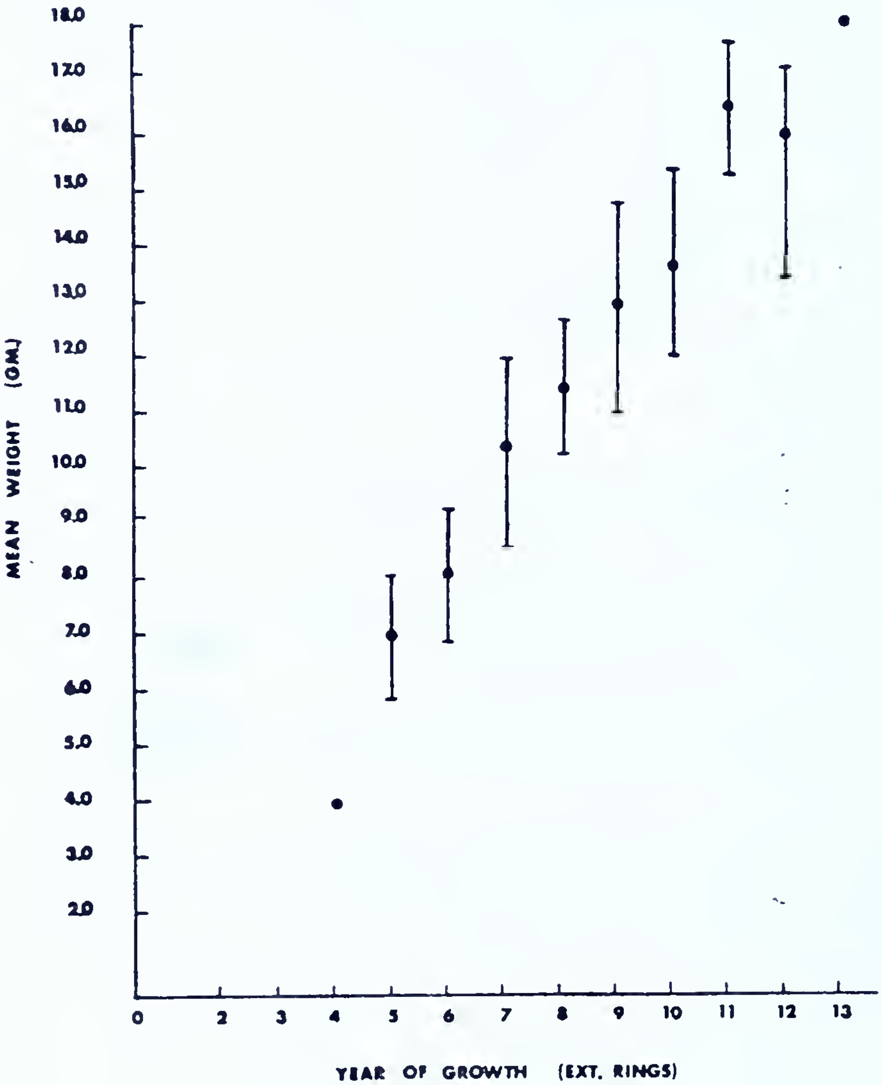


Fig. 18 Frequency distribution of standard deviations of mean shell weight of Discovery Bay population. Vertical lines indicate one standard deviation on either side of the mean represented by solid circles.

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This investigation was initiated as part of an undergraduate honor's thesis completed at the University of Washington under the supervision of Dr. Richard W. Casteel. Dr. Stephen W. Robinson greatly assisted in the computer analysis of the data and photography of the specimens. Mr. James W. Hendel of the University of

California, Berkeley Scientific Photography Laboratory prepared the photomicrographs. Dr. W. B. N. Berry, Dr. Daryl P. Domning, C. Bruce Hanson, Jens Munthe, and Michael J. Novacek offered advice and criticisms which greatly improved the text.

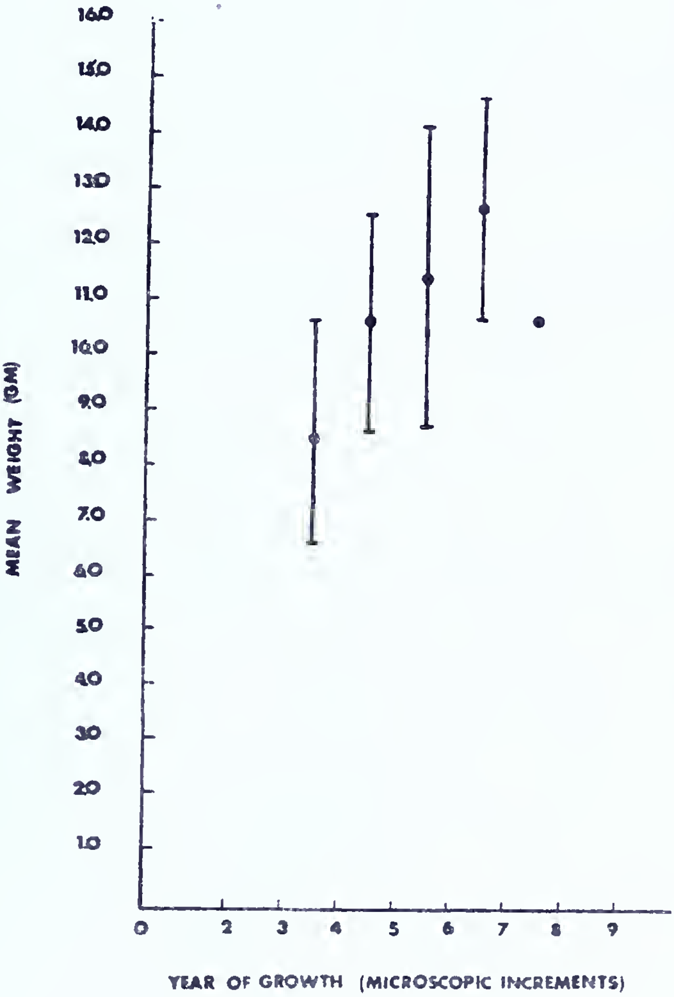

Fig. 19 Frequency distribution of standard deviations of mean shell weight of Discovery Bay population of *Protothaca staminea*. Vertical lines indicate one standard deviation on either side of the mean represented by solid circles.

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IDENTIFICATION OF THE NATIVE CYPRINIDS (PISCES: CYPRINIDAE) OF CALIFORNIA BASED UPON THEIR BASIOCCIPITALS[1]

BY

RICHARD W. CASTEEL[2]

ABSTRACT

The forms of the basioccipitals of the native Cyprinidae of California were investigated in order to assess the value of this bone for identification of genus and species. Seven major types of masticatory processes were identified and these, in combination with characters of the basioccipital as seen in lateral aspect, provide a means for identifying most of the genera, species, and, in some cases, subspecies of native California cyprinids. A key is provided and illustrations of the basioccipitals of the native California cyprinids in ventral and lateral views are presented.

INTRODUCTION

The basioccipitals of the cyprinids (minnows) often occur as fossils and sub-fossils in freshwater deposits. Their use for identification of cyprinid genera and species has been widespread both in North America (Linder and Koslucher, 1974; Smith, 1963; Uyeno, 1960) and the Soviet Union (Inostrantsev, 1882; Lebedev and Lapin, 1954; Lebedev and Tsepkin, 1960; Markevich and Tsepkin, 1969; Nikol'skii, 1935; Shpet, 1949; Tsepkin, 1964; Zhiteneva, 1965, 1966, 1968). Many cyprinids offer valuable information concerning the characteristics of the bodies of water in which they lived.

Differences in form of the basioccipitals among the native cyprinids of California (see Table 1) allow an attempt to identify characters and combinations of characters that are distinctive at the generic and, where possible, at the species level. This study is a preliminary step in the analysis of morphological variation between these species and genera. Its primary aim is to illustrate the basioccipitals of various native Cyprinidae and to facilitate their correct identification. Although Hopkirk (1974) included detailed descriptions of the basioccipitals of six native genera in his sections entitled "Cranial Osteology," no attempt was made to illustrate them or prepare a key to their identification. Some of the species dealt with here are either extinct (for example, *Gila crassicauda* [Miller, 1961, 1963]) or increasingly difficult to obtain in modern collections owing to severe declines in population. These same species are, however, often found in skeletal form during paleontological and archaeological investigations, and for this reason, a presentation of the various forms of their basioccipitals is desirable.

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As a secondary feature, an artificial key to the basioccipitals of the genera, species, and some subspecies of the California cyprinids is presented to aid in the identification of isolated skeletal material.

It appears that the general form of the basioccipital remains relatively unaltered throughout ontogeny. Minor changes in the form of the basioccipital do occur (Figure 1), but these do not appear to hinder identification. Other investigators (Evans and Deubler, 1955; Nikolsky, 1963) have documented changes in the form of pharyngeal teeth with age and variations in feeding behavior. Since the basioccipital is intimately associated with the pharyngeals, some concomitant changes should occur in this bone.

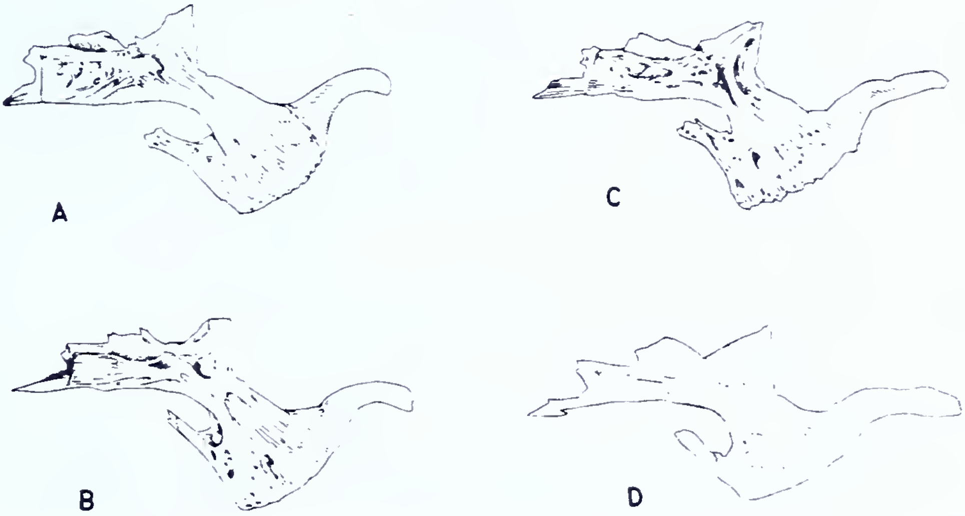

Fig. 1. Basioccipitals of *Orthodon microlepidotus* at various stages of ontogeny. A. Specimen 5163, live weight 759 g, x1; B. Specimen 5174, live weight 423 g, x1.25; C. Specimen 5175, live weight 119 g, x2; D. Specimen 5086, live weight 11 g, x3.5.

MATERIAL AND METHODS

Most of the native cyprinids were available in quantities sufficient to allow examination of numerous size ranges within a single species, but some could be studied only from a pair of individuals of the same species. Every attempt was made, however, to obtain individuals of various sizes from each species.

The key emphasizes the lateral profile of the basioccipital and the form of its masticatory process (Figures 2-4). Weisel (1955) noted the value of the form of the masticatory process of the basioccipital as a species character. The terms used to describe the topography of the basioccipital are taken largely from Harrington (1955). The seven general forms of masticatory processes used in this study are (see Figure 4):

Type 1 - a roughly rectangular form characteristic of the genus *Ptychocheilus;*
Type 2 - an oval form characteristic of the genera *Orthodon* and *Lavinia;*
Type 3 - a spheroidal form, truncated at its anterior end, occasionally with a median projection on the anterior end. This type is characteristic of the genera *Mylopharodon* and *Gila;*
Type 4 - roughly cruciform with a tapering posterior end and slightly square to rounded lateral arms. This type is characteristic of the genus *Hesperoleucus* and certain members of the genus *Gila;*
Type 5 - a subsquare to rounded form characteristic of some members of the genera *Gila* and *Hesperoleucus;*
Type 6 - a roughly pentagonal form with concave margins characteristic of the genus *Pogonichthys*; and
Type 7 - a slightly square to roughly triangular form generally characterized by the posterior projection of the two lateral arms, producing a tricuspid pattern. This type is characteristic of members of the genera *Rhinichthys* and *Richardsonius*.

Uyeno (1960:32) utilized the form of the basioccipital in his study of the genus *Gila* and other North American cyprinids and concluded that "The form of the basioccipital shows wide intra- and inter-specific variability among the fishes examined." That inter-specific variability is great is readily conceded, and, indeed, this variability forms the basis of the present study. Intra-specific variability does exist, as illustrated in Figure 1, but it is not sufficiently great to impair identifications. The present study may help establish a base for paleontological study of Cenozoic cyprinids by stressing osteological characteristics.

Specimen numbers refer to the author's private collection.

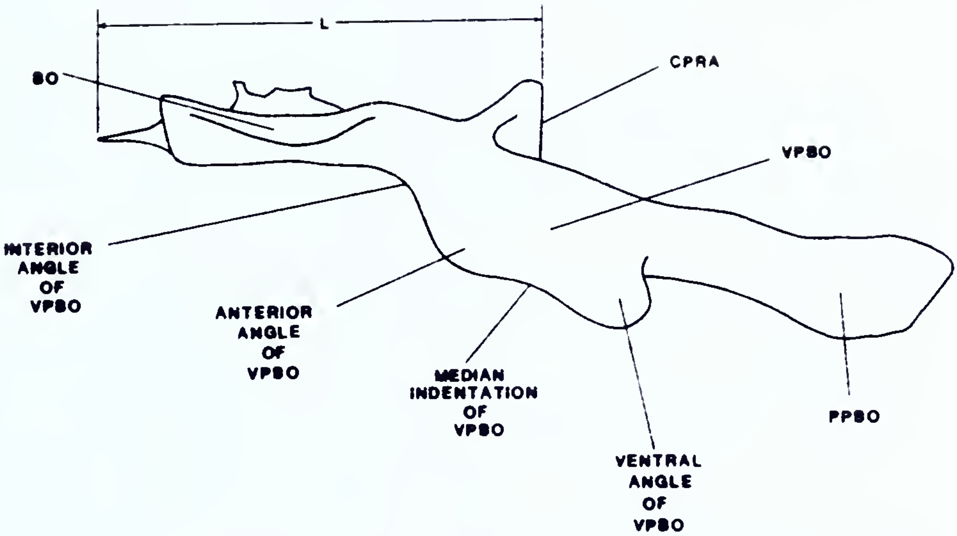

Fig. 2. Basioccipital of generalized cyprinid (lateral aspect). CPRA, centrum of proatlas vertebra. VPBO, ventral portion of basioccipital. BO, basioccipital. PPBO, posterior process of basioccipital. L, length of dorsal portion of basioccipital.

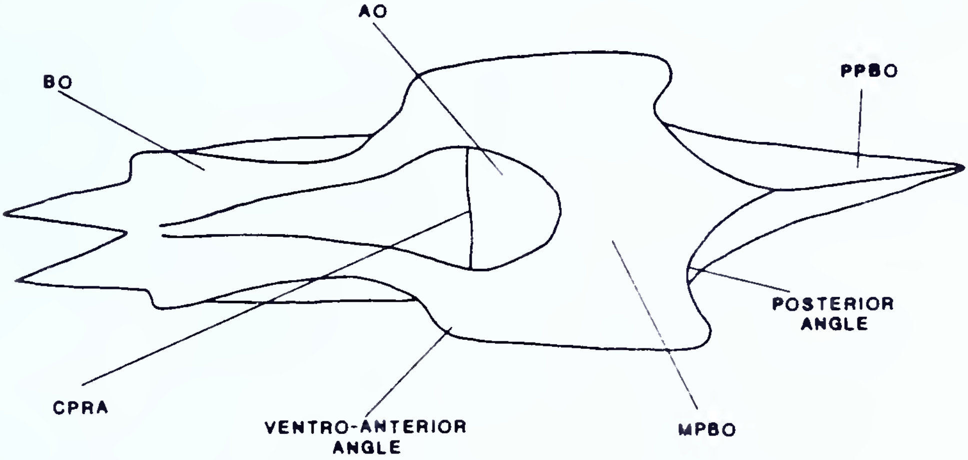

Fig. 3. Basioccipital of generalized cyprinid (ventral view). AO, canal for aorta. MPBO, masticatory plate. BO, dorsal portion. PPBO, pharyngeal process, CPRA, centrum of proatlas vertebra.

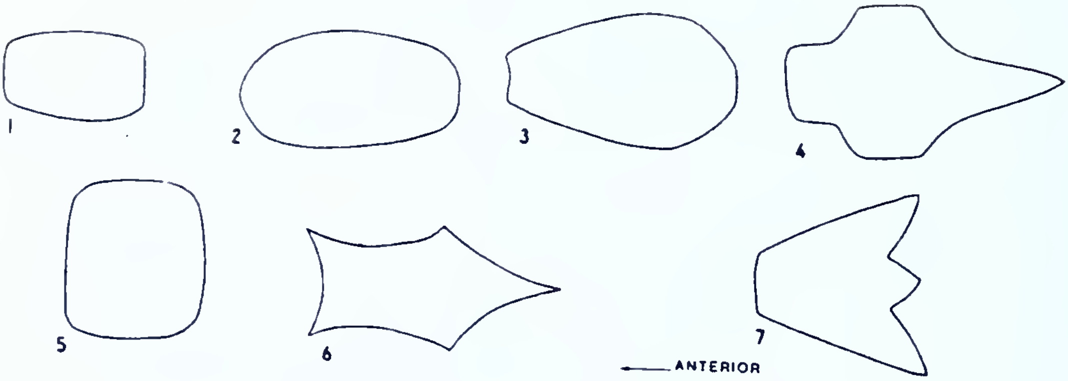

Fig. 4. Ventral view of generalized types of masticatory plates of basioccipital.

A KEY TO THE BASIOCCIPITALS OF THE NATIVE CYPRINIDAE OF CALIFORNIA

The key to the basioccipitals of the native Cyprinidae of California stresses the form of the bone in lateral and ventral aspects. The basioccipitals of each genus and species identified in the key, as well as those of a number of subspecies, are illustrated in Figures 5-10. The fish names follow those of Bailey (1970) and Hopkirk (1974).

1. a) Masticatory plate type 1.........*Ptychocheilus* (Squawfish) (Figure 5A, B)

   b) Masticatory plate not type 1.............................2

2. a) Masticatory plate type 6.................................. ....*Pogonichthys macroledidotus* (Splittail) (Figure 5C)

   b) Masticatory plate not type 6.............................3

3. a) Masticatory plate type 2.................................4

   b) Masticatory plate not type 2.............................5

4. a) Length of ventral process approximately equal to length of dorsal portion of basioccipital; pharyngeal process in form of ventrally concave spur; large, fenestrated spur projecting antero-dorsally from base of masticatory plate....... ....*Orthodon microlepidotus* (Sacramento Blackfish) (Figure 5D)

   b) Length of ventral process less than length of dorsal portion; pharyngeal process not ventrally concave; anteroventral face of ventral process biconcave................ ....*Lavinia exilicauda* (Hitch) (Figure 6A,B)

5. a) Masticatory plate type 3..............................6

b) Masticatory plate not type 3..........................8

6. a) Ventral process very short; masticatory plate large and shield-shaped with anteriorly directed process; masticatory plate with acute ventro-anterior angle....... ....*Mylopharodon conocephalus* (Hardhead) (Figure 6C)

b) Ventral process long; masticatory plate without acute ventro-anterior angle.................................7

7. a) Anteriorly directed process present on masticatory plate..*Gila* (including the species *G. bicolor* [Tui chub], *G. crassicauda* [Thicktail chub], *G. elegans* [Bonytail], and *G. mohavensis* [Mohave chub]). (Figure 7A-D)

b) Anteriorly directed process absent from masticatory plate..*Gila* (including the species *G. bicolor* and *G. mohavensis* only). (Figure 7A, C)

8. a) Masticatory plate type 4..............................9

b) Masticatory plate not type 4..........................10

9. a) Steplike projection present on dorsal margin of pharyngeal process..................*Gila orcutti* (Arroyo chub) (Figure 8A)

b) Steplike projection absent on dorsal margin of pharyngeal process.......*Hesperoleucus symmetricus* (California roach) (including the subspecies *H. s. symmetricus, H. s. venustus, H. s. navarroensis,* and *H. s. parvipinnis*). (Figure 8B-E)

10. a) Masticatory plate type 5.............................11

b) Masticatory plate type 7.............................. ....*Rhinichthys osculus* (Speckled dace) (including its subspecies [Figure 9A-C] and *Richardsonius egregius* (Lahontan redside) [Figure 9D]).

11. a) Masticatory plate extending posteriorly beyond posterior face of centrum of proatlas vertebra.................... ....*Gila coerulea* (Blue chub) (Figure 10A)

b) Masticatory plate not extending posteriorly beyond posterior face of centrum of proatlas vertebra........... ....*Hesperoleucus symmetricus subditus* (Figure 10B)

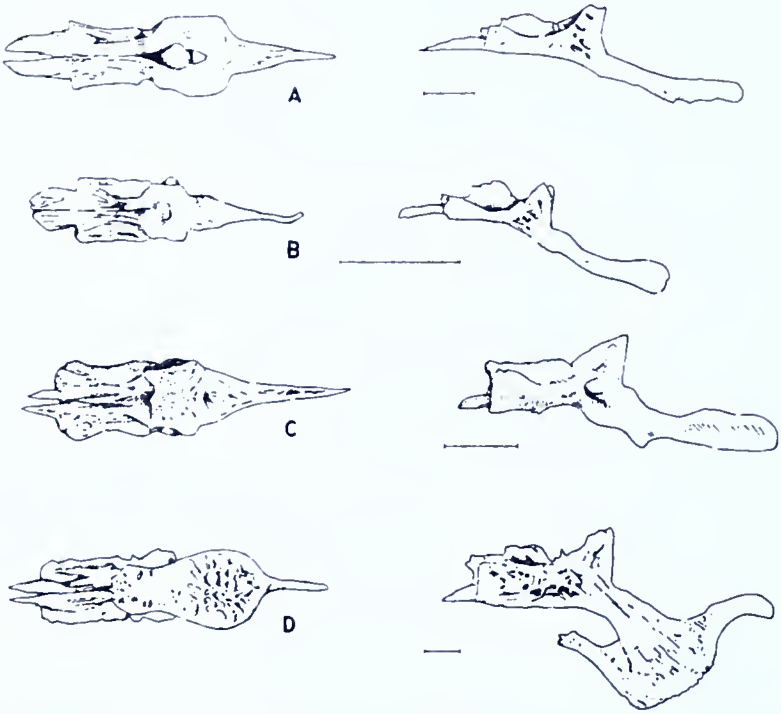

Fig. 5. Basioccipitals of native Cyprinidae of California in ventral and left lateral views. All scales equal 5 mm. A. *Ptychocheilus grandis*, specimen 5257, B. *P. lucius*, specimen 5581, C. *Pogonichthys macrolepidotus*, specimen 5199, D. *Orthodon microlepidotus*, specimen 5163.

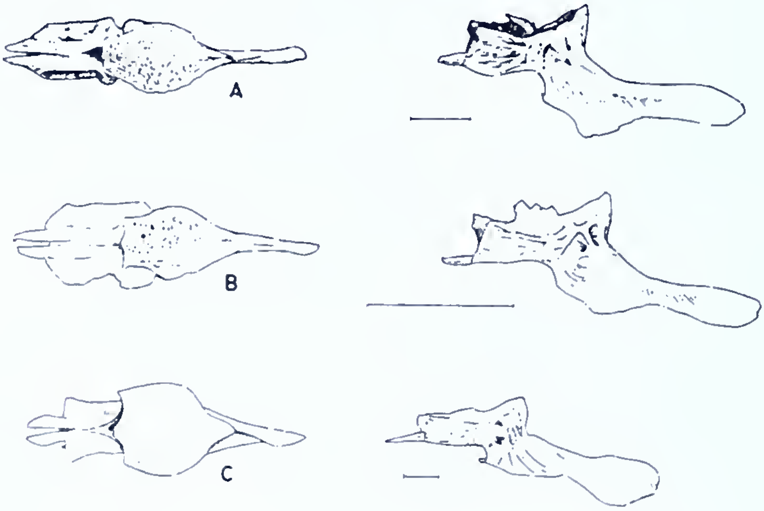

Fig. 6. Basioccipitals of native Cyprinidae of California in ventral and left lateral views. All scales equal 5 mm. A. *Lavinia exilicauda exilicauda*, specimen 5121, B. *L. e. harengus*, specimen 5545, C. *Mylopharodon conocephalus*, specimen 5025.

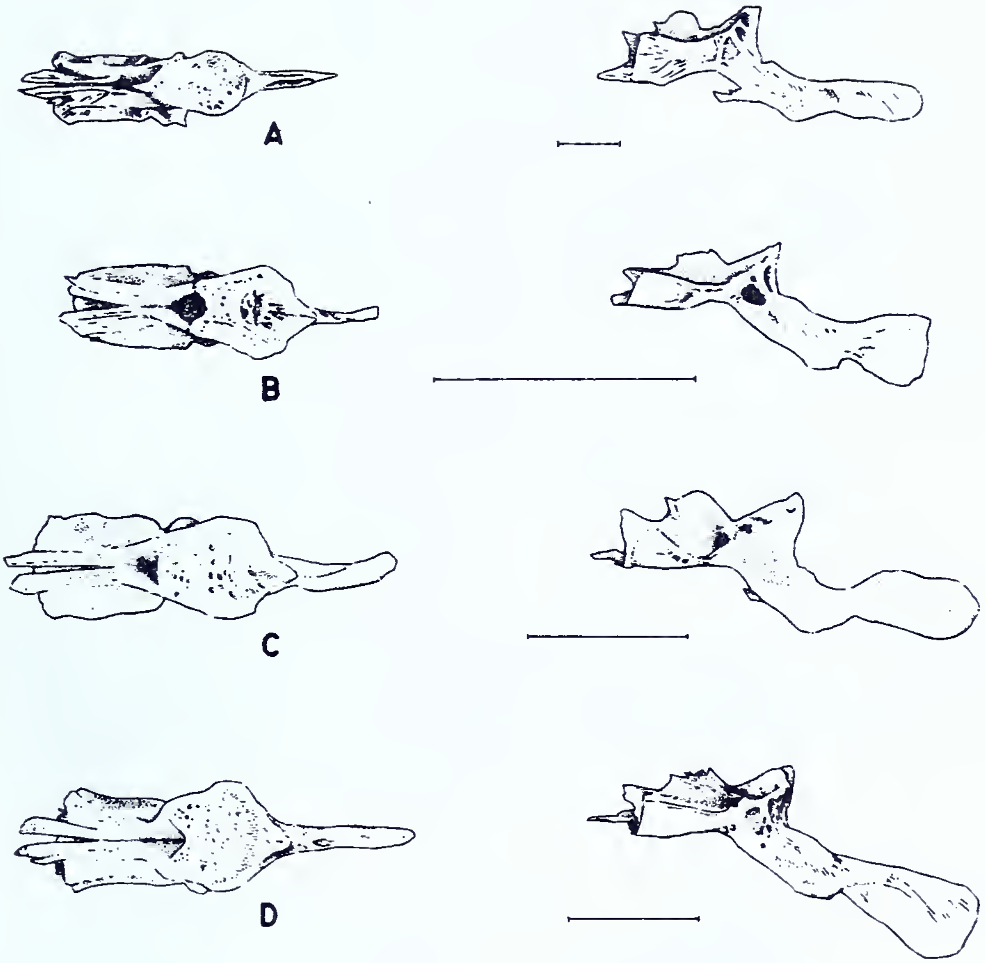

Fig. 7. Basioccipitals of native Cyprinidae of California in ventral and left lateral views. All scales equal 5 mm. A. *Gila bicolor*, specimen 5438, B. *G. crassicauda*, specimen 5592, C. *G. mohavensis*, specimen 5526, D. *G. elegans*, specimen 5595.

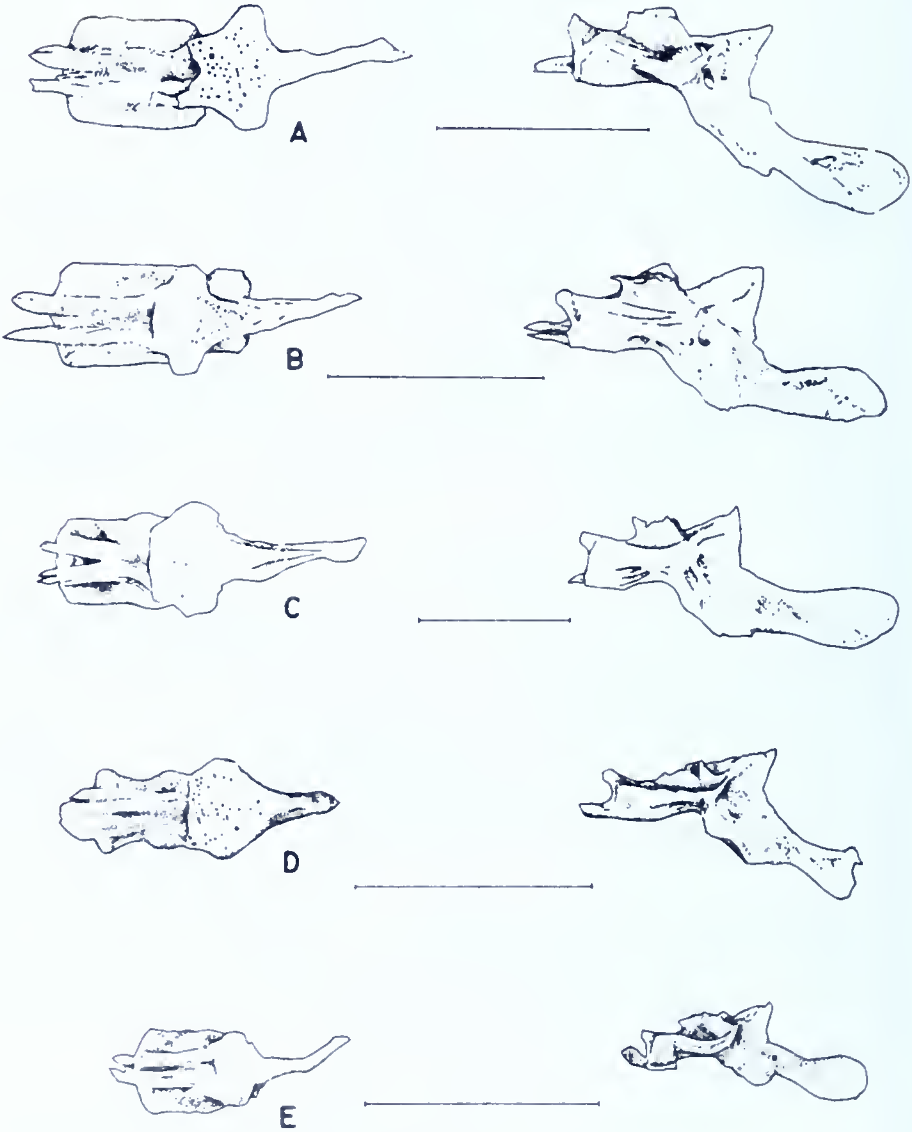

Fig. 8. Basioccipitals of native Cyprinidae of California in ventral and left lateral views. All scales equal 5 mm. A. *Gila orcutti*, specimen 5537, B. *Hesperoleucus symmetricus symmetricus*, specimen 5269, C. *H. s. venustus*, specimen 5248, D. *H. s. navarroensis*, specimen 5543, E. *H. s. parvipinnis*, specimen 5538.

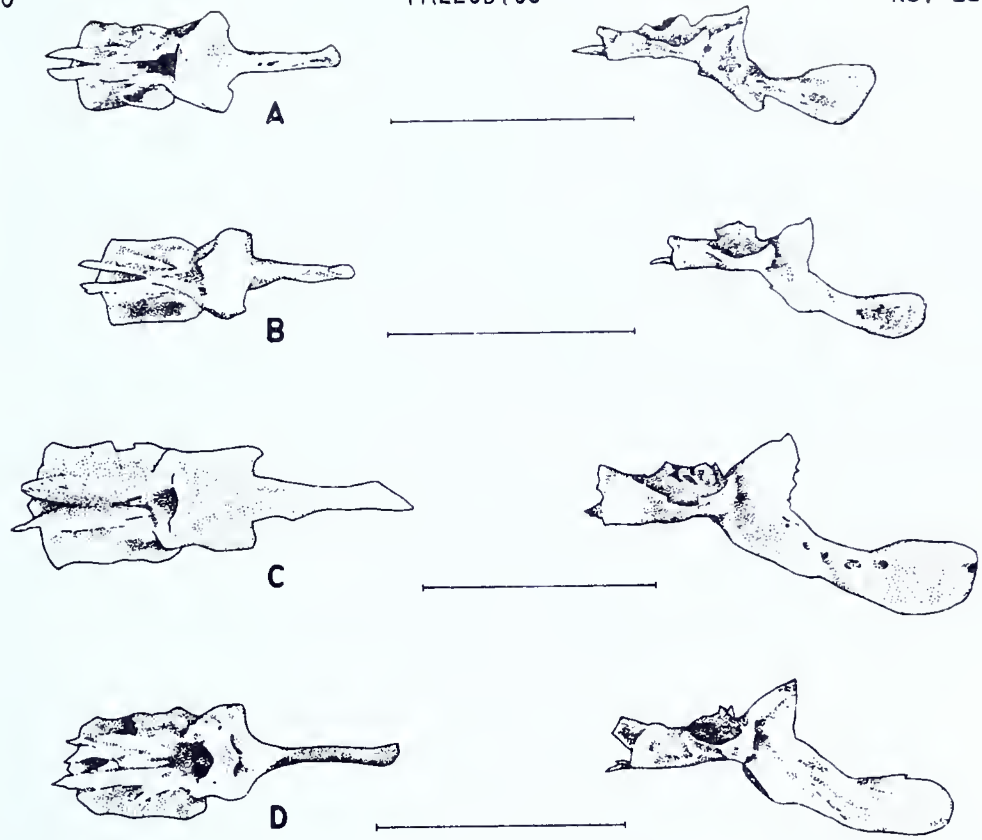

Fig. 9. Basioccipitals of native Cyprinidae of California in ventral and left lateral views. All scales equal 5 mm. A. *Rhinichthys osculus nevadensis*, specimen 5531, B. *R. o. klamathensis*, specimen 5529, C. *R. o. robustus*, specimen 5528, D. *Richardsonius egregius*, specimen 5547.

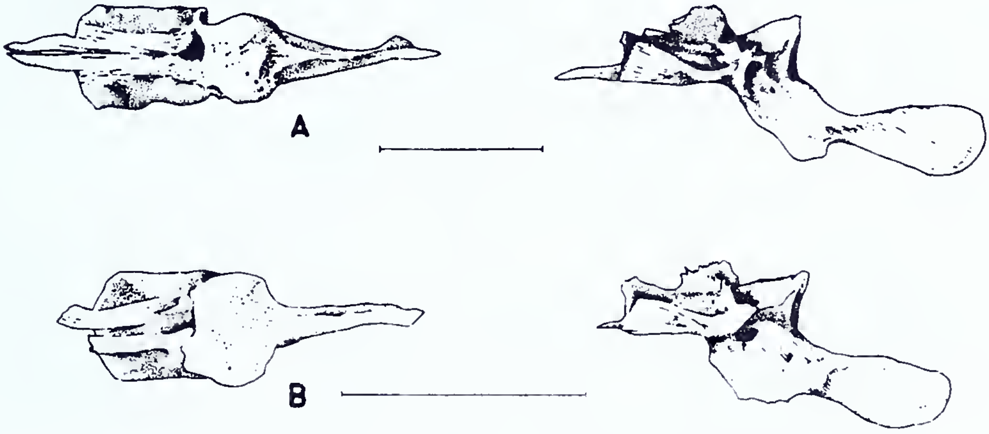

Fig. 10. Basioccipitals of native Cyprinidae of California in ventral and left lateral views. All scales equal 5 mm. A. *Gila coerulea*, specimen 5546, B. *Hesperoleucus symmetricus subditus*, specimen 5540.

Table 1. List of the native Cyprinidae of California (Recent)

Rhinichthys osculus (Girard)	Speckled Dace
Mylopharodon conocephalus (Baird and Girard)	Hardhead
Orthodon microlepidotus (Ayres)	Sacramento Blackfish
Pogonichthys macrolepidotus (Ayres)	Splittail
Lavinia exilicauda (Baird and Girard)	Hitch
Ptychocheilus grandis (Ayres)	Sacramento Squawfish
Ptychocheilus lucius (Girard)	Colorado River Squawfish
Hesperoleucus symmetricus (Baird and Girard)	California Roach
Gila bicolor (Girard)	Tui Chub
Gila mohavensis (Snyder)	Mohave Chub
Gila crassicauda (Baird and Girard)	Thicktail Chub
Gila coerulea (Girard)	Blue Chub
Gila orcutti (Eigenmann and Eigenmann)	Arroyo Chub
Gila elegans (Baird and Girard)	Bonytail
Richardsonius balteatus (Girard)	Lahontan Redside

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I wish to express my sincere thanks to Mr. W. I. Follet and Mrs. Lillian Dempster of the California Academy of Sciences and Dr. J. D. Hopkirk, California State University, Sonoma, for their comments and generosity in making available specimens for this study.

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EVOLUTION OF THE THYLACOSMILIDAE, EXTINCT SABER-TOOTH MARSUPIALS OF SOUTH AMERICA

by

LARRY G. MARSHALL[1]

ABSTRACT

The family Thylacosmilidae, predaceous South American extinct saber-tooth marsupials, includes five species: *Thylacosmilus atrox* Riggs, 1933 (including *T. lentis* Riggs, 1933), of Huayquerian (middle Pliocene) through early Montehermosan (late Pliocene) age; *Notosmilus pattersoni* J. L. Kraglievich, 1960, of Chapadmalalan (latest Pliocene) age; *Hyaenodonops chapalmalensis* Ameghino, 1908, of Chapadmalalan age; *Achlysictis lelongi* Ameghino, 1891, of early Montehermosan and possibly Huayquerian age; and *A. pungens* (Ameghino, 1904) of middle Montehermosan age.

Thylacosmilus atrox and *H. chapalmalensis* are structurally similar and might represent members of a single phylogenetic lineage. The two species of *Achlysictis* might prove synonymous when better known. *N. pattersoni* is problematical and might prove a junior synonym of *H. chapalmalensis*.

The dog-like borhyaenids and saber-tooth thylacosmilids are placed in separate families, the Borhyaenidae and Thylacosmilidae respectively, in the superfamily Borhyaenoidea.

RESUMEN

Se revisa los marsupiales predatores fósiles Sud Americanos (gatos con dientes de sabre), de la familia Thylacosmilidae. Se reconoce cinco especies fósiles: *Thylacosmilus atrox* Riggs, 1933 (que incluye *T. lentis* Riggs, 1933), de edad Huayqueriense (Plioceno medio) hasta Montehermosense temprana finales del Pliocene;

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Notosmilus pattersoni J. L. Kraglievich, 1960, de edad Chapadmalalense (Plioceno cuspidal); *Hyaenodonops chapalmalensis* Ameghino, 1908, de edad Chapadmalalense; *Achlysictis lelongi* Ameghino, 1891, de edad Montehermosense temprana y quizá Huayqueriense; y *A. pungens* (Ameghino, 1904) de mediados del Montehermosense.

Thylacosmilus atrox y *H. chapalmalensis* son muy similares estructuralmente y quizá representen una misma linea filogenética. Es posible que las dos especies de *Achlysictis* resulten sinónimos cuando estan mejor conocidas. *N. pattersoni* es problemática y quizá resulte sinónimo júnior de *H. chapalmalensis*.

Se asigna los borhyaenidos que semejan canes y los thylacosmilidos que semejan gatos con dientes de sabre a dos familias diferentes, Borhyaenidae y Thylacosmilidae respectivamente, dentro de la superfamilia Borhyaenoidea.

INTRODUCTION

The discovery of large predaceous marsupial saber-tooths in Pliocene deposits of Argentina was first announced by Riggs (1929: 117) and the material described in two subsequent papers (Riggs, 1933, 1934). One genus, *Thylacosmilus*, and two species, *T. atrox* and *T. lentis*, were named on the basis of nearly complete cranial and associated post-cranial elements. *Thylacosmilus* was placed in a new subfamily, Thylacosmilinae, of the Borhyaenidae. A second genus, *Notosmilus*, was later added to this subfamily (J. L. Kraglievich, 1960).

For the past two years I have been working on a revision of the family Borhyaenidae. As many of the early named taxa of this group are poorly known and/or lack detailed description, it should be no surprise that three species previously referred to the Borhyaeninae and named by the eminent Argentine paleontologist Florentino Ameghino prove members of the saber-tooth lineage. It is only in hind sight and with aid of the relatively complete material described by Riggs that the affinities of these taxa could be recognized. In addition, search of museum collections in Argentina revealed undescribed materials referable to the Thylacosmilidae.

ABBREVIATIONS USED

FMNH = Field Museum of Natural History, Chicago.
MACN = Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina.
MLP = Museo de La Plata, La Plata, Argentina.
MMP = Museo Municipal de Ciencias Naturales, Mar del Plata, Argentina.
L = Length
W = Width
ca. = approximate measurement

All measurements are in millimeters (mm) unless indicated otherwise.

PROVENANCE OF SPECIMENS

Remains of thylacosmilids have been recovered from six localities within Argentina (Fig. 1). These localities are widely scattered, making correlations difficult and often tentative. In addition, study of stratigraphy and usage of nomenclature have had long and confused histories. It is beyond the scope of this paper to review these problems in detail, but a few preliminary comments are necessary to clarify the site of origin of the specimens and their relative ages. Several excellent works attempt correlation of South American Land Mammal Ages and principal stratigraphic units within Argentina (*e. g.*, Simpson, 1940; Pascual, Hinojosa, Gondar and Tonni, 1966; Pascual and Odreman Rivas, 1971, 1973; and Patterson and Pascual, 1972). I will deal only with those localities pertinent to this study. All are presently regarded as Pliocene in age.

For ease of discussion the localities and lithostratigraphic units are divided into three groups, following the approach employed by Pascual and Odreman Rivas (1973:297). These are: 1) the Western Area, 2) the Area of the Chaco-Bonaerense Plain, and 3) the Mesopotamian Area.

1. Western Area. An important sequence of late Tertiary beds occurs in the Santa María Valley in northern Catamarca and southern Salta, and in nearby parts of central Catamarca Province (Simpson, 1940:667). Four stratigraphic units are currently recognized in this area; from oldest to youngest, these are: the Corral Quemado, Andalgalá, Chiquimil A and Chiquimil B. Thylacosmilids have been recovered from the oldest two (Fig. 2).

The mammalian fauna of the Corral Quemado Formation has been assigned an early Montehermosan Age (Fig. 2). Similarly, the fauna of the Andalgalá is assigned to the Huayquerian Age, and those of the Chiquimil A and B tentatively to the Chasicoan Age (Pascual and Odreman Rivas, 1973). The preliminary faunal lists presented by Riggs and Patterson (1939) are fairly extensive for the Corral Quemado and what is now called the Andalgalá (their Araucanense), but very poor for either part of the Chiquimil (Simpson, 1974:5). Complete and revised descriptions of these faunas have not been published.

As noted by Simpson (1974:5) the Corral Quemado is stratigraphically higher than the Andalgalá and is hence somewhat later. Although the faunal lists are not identical, Simpson does not feel they demonstrate significant differences in age and they might reflect merely the fortunes of collecting or possibly ecological differences. Simpson elected to provisionally consider both formations and their faunas as Huayquerian in age.

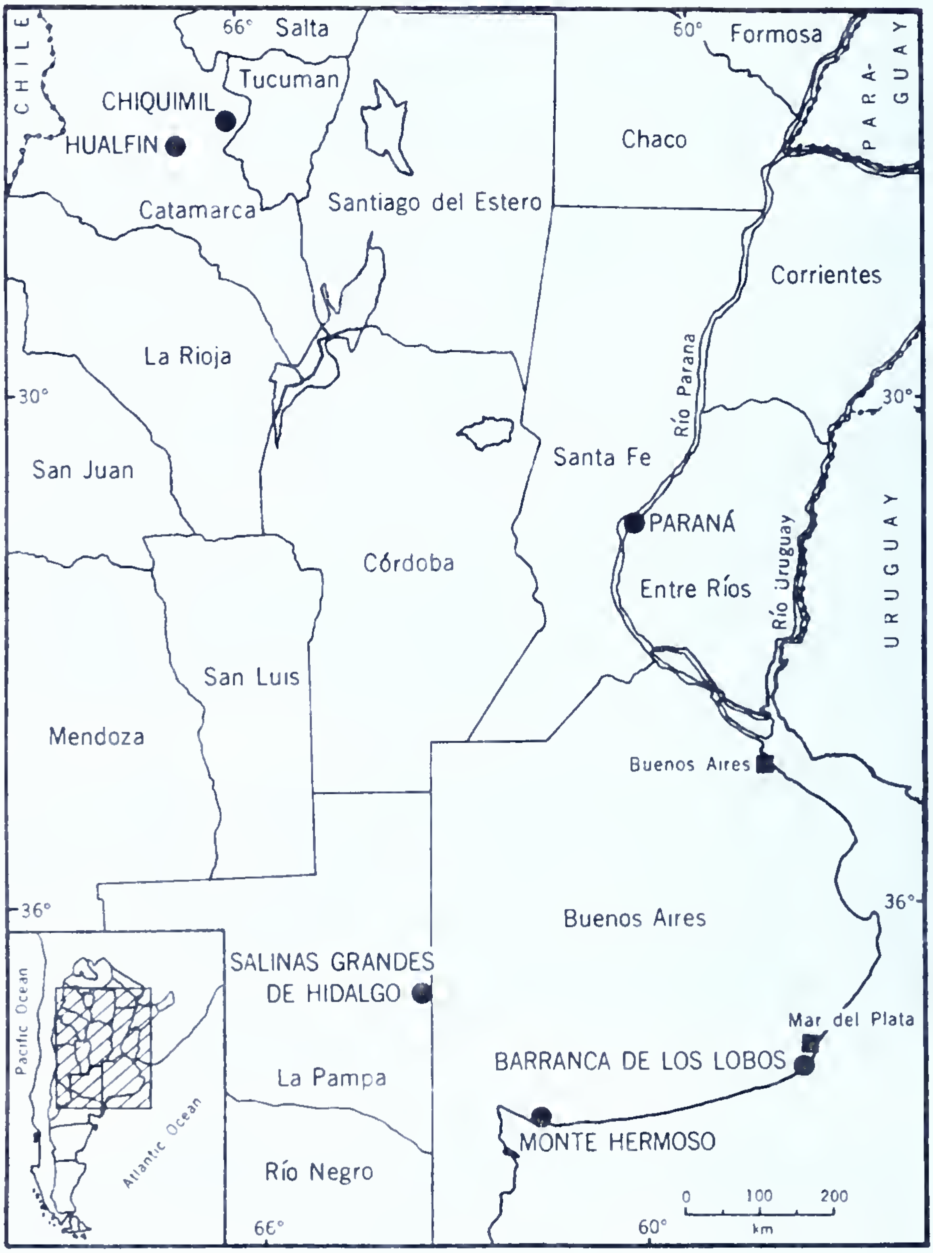

Fig. 1. Map of northern Argentina and some adjacent territory showing localities of Pliocene mammal-bearing beds mentioned in the text.

South American Land Mammal Ages		Western Area	Area of the Chaco-Bonaerense Plain	Mesopotamian Area
PLIOCENE	Chapadmalalan		Fm. Chapadmalal•	
	Montehermosan	Fm. Corral Quemado•	Fm. Monte Hermoso•	'Entrerriense'•
	Huayquerian	Fm. Andalgalá•	Fm. Epecuén•	'Mesopotamiense'•
	Chasicoan	Chiquimil A Chiquimil B	Fm. Arroyo Chasicó	

•Thylacosmilidae recorded

Fig. 2. Correlation of South American Land Mammal Ages and Principal Lithostratigraphic Units for the Pliocene of Argentina (slightly modified from Pascual and Odreman Rivas, 1973). Wavy line represents probable unconformities.

II. Area of the Chaco-Bonaerense. Remains of thylacosmilids are recorded from three localities in this area. One is in the Epecuén Formation in the high cliffs of the Salinas Grandes de Hidalgo, La Pampa Province, about 10-15 km to the south of the railroad station of Salinas Grandes de Hidalgo. The fauna from this horizon is similar to, but slightly older than, the Huayquerias fauna of Mendoze Province, and that from the Andalgalá Formation of Catamarca Province (Pascual and Bocchino, 1963:100; Zetti, 1972).

A large vertebrate fauna including thylacosmilids is known from the Monte Hermoso Formation at Monte Hermoso, along the Atlantic coast just east of Bahía Blanca, and another from the Chapadmalal Formation along the shore of the Atlantic Ocean between Mar del Plata and Miramar. Beds with diagnostic mammals are not yet known in a continuous section, but the faunas demonstrate beyond doubt that the Monte Hermoso beds are older than those of the Chapadmalal (Simpson, 1940:670).

For many years it was customary (*e.g.*, Simpson, 1940) to regard each of these faunas as representing the type of a distinct age, hence the Montehermosan and Chapadmalalan, respectively. Recently, Pascual *et al.* (1966), and Pascual and Odreman Rivas (1971, 1973) restudied the faunas of the Chapadmalal and Monte Hermoso Formations. They found them to differ less than had usually been believed (Ameghino, 1888, 1889, 1904; and L. Kraglievich, 1934), and proposed that the Chapadmalal Formation be included within the Montehermosan Age. Simpson (1972:4) recommended retention of the designation Chapadmalalan, not in confirmed opposition to the views of Pascual and his fellow workers, but simply because no one has yet reanalysed the meticulous work of L. Kraglievich (1934) on which the supposed distinction mainly rests.

III. Mesopotamian Area. A late-Tertiary (Pliocene) vertebrate fauna of "mixed" character has been collected from sediments along the east bank of the Río Paraná, near the city of Paraná, Entre Ríos Province, Argentina. The predominant faunal elements indicate a Huayquerian age, but there are rare forms that might be reworked from older deposits of Santacrucian and/or Chasicoan age, and a few others which are representatives of Montehermosan age (Pascual and Odreman Rivas, 1971:404).

The fossiliferous beds in this area have received numerous names and the applied nomenclature is confusing and disputed (see Reig, 1957:224; Bianchini and Bianchini, 1971:3). Basically there appears to be a mixture of marine and terrestrial facies. The name "Entrerriense" has generally been applied to the somewhat younger marine facies, which contain some terrestrial vertebrates, while the predominant fluviatile facies has been generally included under the name "Mesopotamiense" (Pascual and Odreman Rivas, 1971:404). According to Pascual and Odreman Rivas (1973, chart opposite p. 318) fosiles from the "Entrerriense" are generally correlated with beds of Montehermosan age, while fossils from the older "Mesopotamiense" are tentatively correlated with Huayquerian faunas. There are no relevant radiometric dates or geomagnetic correlations yet available, and most faunas studies are in need of revision.

In this study (Fig. 2) I have followed the faunal correlations proposed by Pascual and Odreman Rivas (1973), except for recognizing a separate Chapadmalalan Age (upper part of Montehermosan Age of Pascual and Odreman Rivas), following the reasonable recommendations to do so as outlined by Simpson (1972:4).

SYSTEMATICS

In recent years it has been practice to include all large South American predaceous marsupials in one family, the Borhyaenidae. There has been, however, debate about the affinities, classification and subdivision of this group. These issues are summarized by Simpson (1948:38). It is generally accepted that the Borhyaenidae evolved in South America from didelphid-like ancestors. The family has been conveniently divided into two subfamilies, the diverse dog-like Borhyaeninae and the rarer saber-tooth Thylacosmilinae (Simpson, 1971:113). The family Borhyaenidae was at one time included in its own superfamily Borhyaenoidea (*e. g.* Simpson, 1945:42), although that same author has recently (1971:113) opted for placing the Borhyaenidae in the Didelphoidea.

During my study of borhyaenids it became evident that this classification no longer adequately expresses the phylogenetic relationships or diversity of the group. I choose to elevate the subfamilies Borhyaeninae and Thylacosmilinae to full family rank and place them in their own superfamily Borhyaenoidea.

Justification for this arrangement stems from several lines of evidence. First, the differences between the borhyaenids and thylacosmilids are equal to or even greater than that existing between recognized families of placental mammals.

Secondly, within the borhyaenids there exists greater diversity than previously recognized. Several lines of evolution within this group can be confidently traced in the fossil record, and they warrant recognition at the subfamily level. The differences between these subfamilies, which are real and can be demonstrated, are less than those existing between them and thylacosmilids.

Thirdly, the Borhyaenidae and Thylacosmilidae are placed in the superfamily Borhyaenoidea as they clearly represent an evolutionary unit distinct from the Didelphoidea. There is every reason to believe that thylacosmilids evolved from borhyaenids or from a borhyaenid-like ancestor.

Lastly, the present classification better expresses the diversity of this group, and by extension, the Marsupialia. Evidence supporting these assertions will appear in a comprehensive review of the Borhyaenidae which is now in preparation (Marshall, ms.).

Superorder MARSUPIALIA Illiger, 1811:75

Order MARSUPICARNIVORA Ride, 1964:99

Superfamily BORHYAENOIDEA Simpson, 1930:9

Diagnosis.--I^{0-4}_{0-3} C^{1}_{1} P^{2-3}_{2-3} M^{4}_{4}. South American predaceous marsupials of small to large size. Lack palatal vacuities. Transverse canal either very reduced or absent. Strong sagittal and nuchal crests. Lunar small and in contact with large magnum. Lacrimal extends onto rostrum and usually has large tuberosity developed above lacrimal canal. Lacrimal canal opens within orbit.

Family BORHYAENIDAE Ameghino, 1894:371

Diagnosis.--I^{3-4}_{2-3} C^{1}_{1} P^{3}_{3} M^{4}_{4}. Small to large size. Rostrum usually robust and well developed. Upper and lower canines laniary and usually with closed pulp cavities in adults. Mandibular symphysis usually shallow (may be fused or unfused in adults) and without flange. Mandibular ramus of subequal depth and breadth below molar series, and without distinct labial bend posteriorly along ventral edge. Masseteric fossa shallow. Premolars all double rooted. Molars usually increase rapidly in size from M_1 to M_4. Protocone moderate or reduced. Paracone often reduced, and paracone and metacone approximated on M^{1-3}.

Talonids large or reduced and often imperfectly or not basined. Metaconids usually absent and always smaller than paraconids. Nasolacrimal contact broad. Nasals large and expanded posteriorly. Orbit open posteriorly. Basicranial and basifacial planes parallel. Entepicondylar foramen present.

Distribution.--Beds of Riochican (late Paleocene) through Montehermosan (late Pliocene) age; Argentina, Bolivia, Brazil, and Colombia, South America.

Family THYLACOSMILIDAE (Riggs, 1933:65) Marshall, 1976

Diagnosis.--I^{0}_{0} C^{1}_{1} P^{2}_{2} M^{4}_{4}. Large size with massive facial region and short cranium. Upper canines large, deeply anchored, evergrowing sabers. Deep-wide symphyseal flange on mandibular ramus medial to upper canine. Upper molars lack stylar shelf. Protocone absent although anterolingual root present and well developed. Nasolacrimal contact absent. Superior branch of maxillary greatly inflated to accommodate large bases of upper canines which extend backward between orbits to meet at mid-line of skull. Nasal bones long, attenuated and laterally compressed. Occipital condyles strongly projecting. Prominent pair of tubercles developed on basisphenoid. Parocciptial process hyperdeveloped. Auditory bulla present and moderately inflated. External auditory meatus "enclosed" ventrally by contact, but not fusion, of mastoid process with basifacial region. Mandibular ramus shallow below posterior molars, becoming deeper and narrower anteriorly. Ventral border of mandibular ramus with distinct labial bend becoming pronounced posteriorly. Lingual face of ramus with distinct labial bend, becoming larger posteriorly. Lingual face of ramus below M_{3-4} convex, labial face concave. Masseteric fossa restricted, but deep. Lower molars narrow transversely, with paraconid, protoconid and talonid cusp nearly aligned anteroposteriorly (protoconid tends to lie slightly labiad of other two cusps). Metaconid absent. Talonid cusp similar in size and shape to paraconid on anterior molars. Entepicondylar foramen absent. Forefeet digitigrade, hindfeet plantigrade.

Distribution.--Beds of Huayquerian, Montehermosan and Chapadmalalan Age; Catamarca, Buenos Aires, Entre Ríos and La Pampa Provinces, Argentina, South America.

Achlysictis Ameghino, 1891a:147

Achlysictis Ameghino, 1891a:147; L. Kraglievich, 1934:61.
Acrohyaenodon Ameghino, 1904:267; L. Kraglievich, 1934:62; Ringuelet, 1966:54.

Type Species.--*A. lelongi* Ameghino, 1891a:147.

Diagnosis.--Dentition smaller than *Thylacosmilus* or *Hyaenodonops*. Deep pit at anterior edge of masseteric fossa. Talonid cusp large and similar in size and structure to paraconid on anterior molars. Talonid cusp on M_3 about half size of paraconid, and on M_4 about one quarter size of paraconid. Small anterobasal cingulum becomes progressively larger from M_2 to M_4.

Distribution.--Beds of Montehermosan and possibly Huayquerian age, Entre Ríos and Buenos Aires Provinces, Argentina.

Achlysictis lelongi Ameghino, 1891a:147

(Fig. 3; Table 1)

Achlysictis lelongi Ameghino, 1891a:147, Fig. 52 (*partim*); 1891b:249; 1898:190, Fig. 55d; L. Kraglievich, 1934:61; J. L. Kraglievich and Reig, 1954:212.

Type.--MACN 5892, a fragment of a right mandibular ramus with alveoli of M_2 and M_{3-4} complete, but worn. Figured by Ameghino, 1891a, Fig. 52; 1898, Fig. 55d.

Referred Specimens.--MACN 9163, an isolated right M_2; MACN 4070, a fragment of a right mandibular ramus with roots of M_{3-4}; and possibly MACN 2549, a fragment of a right upper canine.

Horizon and Localities.--All four specimens were collected from near the city of Paraná, Entre Ríos Province, Argentina. MACN 9163 is labeled "Entrerriano", and MACN 2549 is labelled "Horizonte Mesopotamiense"; the other two specimens lack specific stratigraphic data.

Age.--Huayquerian and possibly Montehermosan.

Diagnosis.--Slightly smaller than *Achlysictis pungens*.

Measurements.--Table 1. MACN 5892, depth of mandibular ramus below labial side of M_2 = 30.0 mm, breadth of same = 11.5 mm; depth of mandibular ramus below labial side of M_4 = 25.0 mm, breadth of same = 10.0 mm; length of M_{2-4} = 33.2 mm.

Comments.--*Achlysictis lelongi* was referred by Ameghino (1891a:147) to the Creodonta, family Hyaenodontidae. L. Kraglievich (1934:61) later placed it in the marsupial family Borhyaenidae, and more specifically in the subfamily Proborhyaeninae, following the subdivision of the family proposed by Cabrera (1927:273).

The type (MACN 5892) was collected by Sr. Leon Lelong of Paraná and sold to the MACN in 1886. It was later described and figured by Ameghino (1891a:147, Fig. 52). In 1924 the MACN acquired an isolated right M_2 (MACN 9163) from the type locality. This tooth fits into the alveoli of the type and the broken surfaces of the roots interlock perfectly. There is no doubt that they represent one and the same specimen.

L. Kraglievich (1934:62) recorded a fragment of a right canine (MACN 2549) which he tentatively associated with *Achlysictis* or *Stylocynus*. According to the MACN register this specimen was collected from the "Barrancas del Río Paraná, Entre Ríos Formación, Entrerriano". L. Kraglievich (1934:62) referred to an illustration of this canine although the figure was not given. This figure has since been published by his son, J. L. Kraglievich, (1960:67, Fig. 5), and the fossil was compared with canines of *Notosmilus pattersoni* and *Thylacosmilus atrox*. The measurements presented by J. L. Kraglievich (1960:70) clearly show that MACN 2549 is similar in size to *N. pattersoni* and considerably smaller than *T. atrox*. Affinities of this tooth with *Notosmilus* were suggested.

In reference to the work of L. Kraglievich (1934:62), Riggs and Patterson (1939:149) noted, "this specimen [MACN 2549] is a canine of *Thylacosmilus*, or of some closely related genus as yet unknown". This tooth might be referable to *A. lelongi*, and because of the proximity of their localities I have tentatively referred it to that species. It must be remembered, however, that reference of this specimen to *Thylacosmilus* or even *Notosmilus* cannot be completely dismissed.

The type of *A. lelongi* (MACN 5892, by its association with MACN 9163) was collected from the "Entrerriano" horizon, which is considered early Montehermosan in age, while MACN 2549 was collected from the "Mesopotamiense" horizon, which is of Huayquerian age (see Pascual and Odreman Rivas, 1973:318). If MACN 2549 is indeed referable to *A. lelongi* then this species ranges from Huayquerian through early Montehermosan, a range similar to that of *Thylacosmilus atrox* (see below).

In the original description of *A. lelongi* Ameghino (1891a) referred a "penultimate" upper molar to this species and gave its measurements. This specimen (MACN 5893), a fragment of a right maxilla with M^2, roots of M^1 and posterior alveoli of P^3, is in fact referable to *Stylocynus paranensis*. Although Ameghino mentions this specimen first in his description of *A. lelongi*, he distinctly indicated in his catalogue that the ramus fragment (MACN 5892), which he also figured, was the type.

Achlysictis pungens (Ameghino, 1904:267)

(Fig. 4; Table 1)

Acrohyaeondon pungens Ameghino, 1904;267; Rovereto, 1914:150, Fig. 66; L. Kraglievich, 1934:62; Riggs, 1934:3; Ringuelet, 1966:54, Pl. 13, fig. A (*partim*).
Acrohyaenodon fungens (sic) Rovereto, 1914:150, caption to Fig. 66.

Type and Only Specimen.--MACN 7916, two isolated right lower molars, M_2 and M_4, of same individual.

Horizon and Locality.--Monte Hermoso, type locality of Montehermosan, Buenos Aires Province, Argentina.

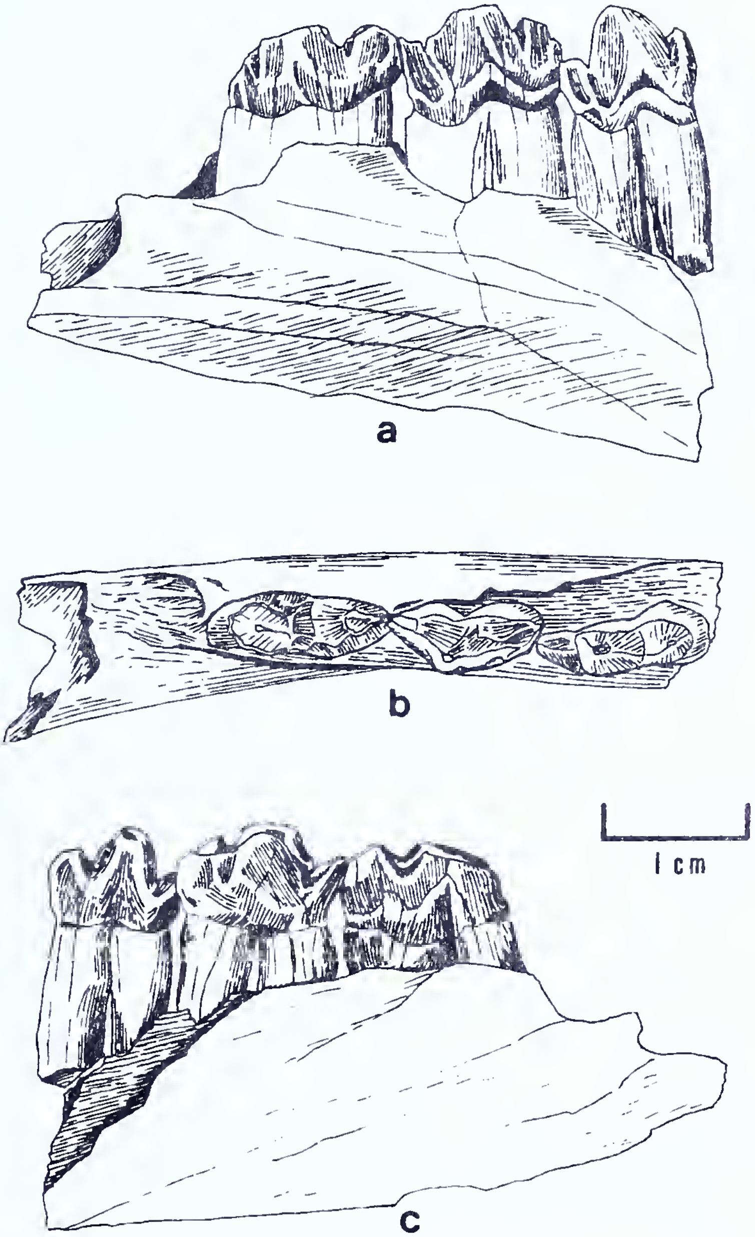

Fig. 3. *Achlysictis lelongi* Ameghino, 1891a:147. Type, MACN 5892, a fragment of a right mandibular ramus with alveoli of M_2 and M_{3-4} complete, but worn; and MACN 9163, in isolated right M_2 (same specimen as MACN 5892): a, labial; b, occlusal; and c, lingual views. Scale = 1 cm.

Table 1. Cheek tooth measurements of species of Thylacosmilidae.

Specimen	M1		M2		M3		M4	
	L	W	L	W	L	W	L	W
Lower dentition								
Achlysictis lelongi								
MACN 5892	...	...	....	...	11.3	5.0	12.4	5.8
MACN 9163	...	...	10.0	4.0	....	...	....	...
Achlysictis pungens								
MACN 7916	...	...	10.0	4.3	....	...	12.8	5.9
Hyaenodonops chapalmalensis								
MACN 6639	...	...	....	...	....	...	13.5	6.0
Thylacosmilus atrox								
*FMNH P14344	9.9	4.4	11.8*ca*	5.1	14.6	7.0	16.4	7.4
Upper dentition								
Thylacosmilus atrox								
*FMNH P14531 (r)	15.6*ca*	9.1	15.4	10.7	20.0	11.8	7.7	8.8
*FMNH P14531 (l)	....	...	16.7	8.9	....	....	...	...
FMNH P14474	11.5	7.2	15.7	9.0	16.0	9.2	7.7	5.6

*Measurements courtesy of Dr. W. D. Turnbull.

Age.--Montehermosan.

Diagnosis.--Slightly larger than *Achlysictis lelongi* (see Table 1).

Description.--The teeth are of a young individual, the cusps are sharp and there is only slight indication of occlusal wear. The posterolingual edges of both teeth are missing.

Comments.--In the transverse narrowness of the molars, structure of the talonid, and orientation of the paraconid, protoconid and talonid cusp in a single anteroposterior axis, this species is virtually identical to *A. lelongi*. *A. pungens* is slightly larger than *A. lelongi* in three of the four dimensions compared in Table 1. These differences are insignificant and of dubious, if any, taxonomic value. These species will probably prove synonymous when better known.

There was no trace in the MACN collection of the fragmentary mandibular ramus containing the M_4 noted by Ameghino (1904:267). The mandibular ramus fragment and the M_4 were surely separated before 1914 when Rovereto (1914, Fig. 66) figured the M_2 and M_4 as they now appear.

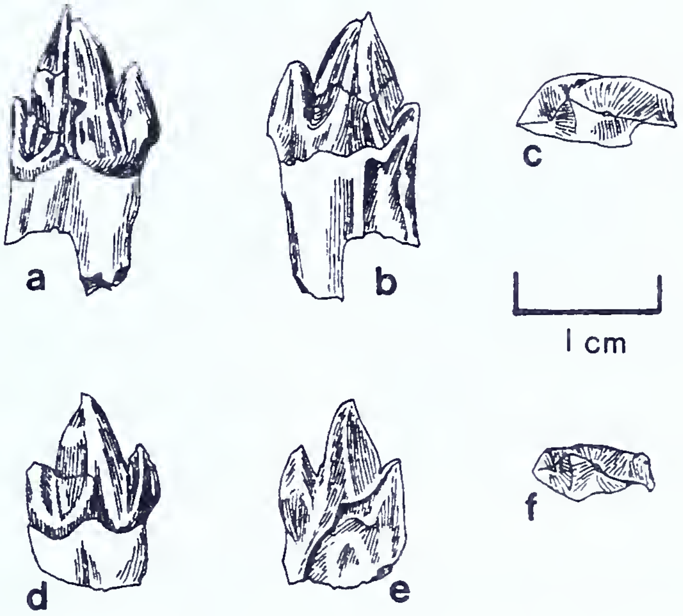

Fig. 4. *Achlysictis pungens* (Ameghino, 1904:267). Type, MACN 7916, two isolated lower molars, M_2 and M_4. a-c, M_4: a, labial; b, lingual; and c, occlusal views. d-f, M_2: d, labial; e, lingual; and f, occlusal views. Scale = 1 cm.

The left M_4 (part of MACN 6203-6265) figured by Ringuelet (1966, Pl. 13, fig. A, far right) was erroneously referred to this species. It is a specimen of *Borhyaena tuberata* (family Borhyaenidae), and is from the Santa Cruz Formation (Santacrucian-middle Miocene) at La Cueva, Santa Cruz Province, Argentina.

Achlysictis paranensis, erected by Ameghino (1886:11) on an isolated right lower canine (MACN cast 1503), was correctly referred by L. Kraglievich (1934:61) to the procyonid genus *Cyonasum* (Order Carnivora). J. L. Kraglievich and Reig (1954:212) suggested that this species is probably synonymous with *Cyonausa argentina*.

Hyaenodonops Ameghino, 1908:423

Hyaenodonops Ameghino, 1908:423; L. Kraglievich, 1934:62.

Type Species.--*Hyaenodonops chapalmalensis* Ameghino, 1908:423.

Diagnosis.--Same as for the type and only known species.

Distribution.--Chapadmalal Formation, Buenos Aires Province, Argentina.

Hyaenodonops chapalmalensis Ameghino, 1908:423

(Fig. 5; Table 1)

Hyaenodonops chapalmalensis Ameghino, 1908:423; Rovereto, 1914:185, Fig. 71; L. Kraglievich, 1934:62; Riggs, 1934:3; Reig, 1958b: 281; J. L. Kraglievich, 1960:63.
?Acrohyaenodon chapalmalensis Reig, 1958a:249.

Type and Only Specimen.--MACN 6639, an isolated left M_4, lacking tip of protoconid.

Horizon and Locality.--Chapadmalal Formation south of Mar del Plata, Buenos Aires Province, Argentina.

Age.--Chapadmalalan.

Diagnosis.--Slightly smaller than *Thylacosmilus atrox*. M_4 transversely narrow. Paraconid about half size of protoconid. Talonid reduced to tiny basal cuspule. Anterobasal cingulum absent.

Description.--The tooth is deeply worn and only the tip of the protoconid is actually broken. Lingually a small ridge connects the talonid cuspule with the posterior face of the protoconid. The roots are curved sharply in a posterior direction. Their bases are bulbous and covered with large nodular rugosities. The posterior deflection of the roots suggests a shallow mandibular ramus below the posterior molars, as is seen in specimens of *Thylacosmilus* and *Achlysictis*.

Comments.--Ameghino (1908:423) originally referred *Hyaenodonops chapalmalensis* to the Creodonta, and Rovereto (1914:185) later included it in the family Hyaenodontidae. Riggs (1934:6) commented that in structure of the lower part of the narrow cleft separating protoconid from paraconid and in the reduced talonid this species was similar to borhyaenids.

Reig (1958a:249) published a faunal list of vertebrate taxa of the Chapadmalal Formation, and within the Thylacosmilinae recorded "*Gen. et sp. nov. (?Acrohyaenodon chapalmalensis)*". He later (1958b: 281) noted, "No encuentro ningún argumento de valor para diferenciar el molar inferior tipo de la especie, del género *Acrohyaenodon* de

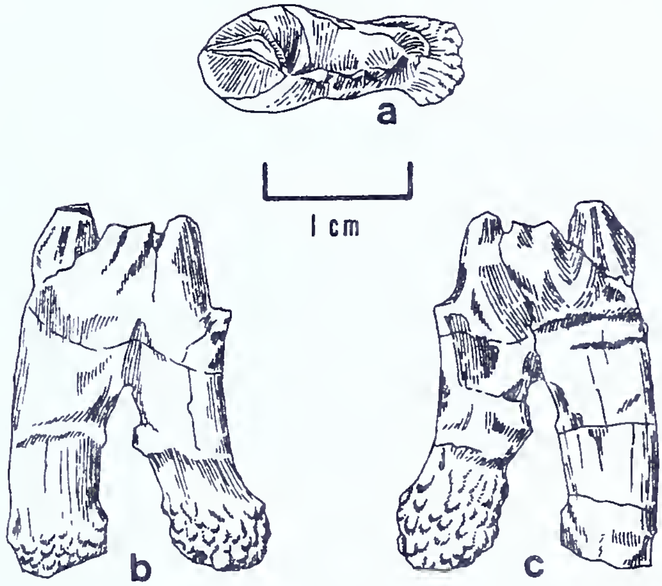

Fig. 5. *Hyaenodonops chapalmalensis* Ameghino, 1908:423. Type, MACN 6639, an isolated left M_4, almost complete: a, occlusal; b, labial; and c, lingual views. Scale = 1 cm.

Monte Hermoso y al parecer también del Plioceno del Valle de Santa María, al que creo que habría que transferir la especie en caso que materiales futuros confirmen su validez."

J. L. Kraglievich (1960:63) was also impressed with the similarity between *Hyaenodonops* and *Acrohyaenodon*. "Creo que, por el tamaño y caracteres de este diente [*H. chapalmalensis*], no es posible, razonablemente, separar el ejemplar de *Acrohyaenodon pungens* ya que las escasas diferencias que se advierten, son asignables a la edad individual y al diferente estado de conservación. Es muy probable que *Hyaenodonops*, al menos, deba pasar a la sinonomia de *Acrohyaenodon*, que, como dije, es un verdadero Borhyaeninae."

The transverse narrowness of M_4, broad lingual basin separating paraconid and protoconid, reduction of talonid to a single basal cuspule, and posterior bend of roots, all show this tooth is from a thylacosmilid, and a form not very different from *Thylacosmilus atrox*. These taxa differ from species of *Achlysictis* in having a paraconid about half the size of the protoconid, in lacking an anterobasal cingulum, and in having a tiny posterobasal talonid cuspule. *H. chapalmalensis* might represent a direct descendant of *T. atrox*.

L. Kraglievich (1934:62) reported that a left ulna lacking the distal and proximal ends (MACN 17249) from the Chapadmalal Formation near Miramar might be referable to *H. chapalmalensis*. Measurements: L = 99.0 mm; anteroposterior diameter of semilunar notch = 22.0 mm.

A second specimen from the same locality consists of a complete right radius (MACN 17250) measuring 111.0 mm in length. Both of these specimens are similar to, but smaller than, elements of *Prothylacynus patagonicus* figured by Sinclair (1906). They are certainly referable to the Borhyaenoidea, although owing to a lack of associated dental elements generic and even familial affinities are uncertain.

Notosmilus J. L. Kraglievich, 1960:55

Notosmilus J. L. Kraglievich, 1960:55.

Type Species.--*Notosmilus pattersoni* J. L. Kraglievich, 1960:56.

Diagnosis.--Same as for the type and only known species.

Distribution.--Chapadmalal Formation, Buenos Aires Province, Argentina.

Notosmilus pattersoni J. L. Kraglievich, 1960:56

(Table 1)

Notosmilus pattersoni J. L. Kraglievich, 1960:56, Figs. 1, 3; Ringuelet, 1966:57, Pl. 10, figs. D-H; Simpson, 1971:112.

Type and Only Specimen.--MMP S-489, a fragment of a right maxilla with root of canine and loose, but associated, tip of a right canine.

Horizon and Locality.--Level VI or VII of the Chapadmalal Formation, Barranca de los Lobos, near Miramar, Buenos Aires Province, Argentina.

Age.--Chapadmalalan.

Diagnosis.--About one half the size of *Thylacosmilus atrox*.

Description.--See J. L. Kraglievich (1960).

Comments.--The large saber-like upper canine with a prominent keel extending along its outer surface; large inflated maxilla; and rudimentary nasals indicate that the type of *N. pattersoni* (MMP S-489) is part of a thylacosmilid. All of these features agree with *Thylacosmilus atrox*. When the type of *N. pattersoni* is superimposed over the left canine of the type of *T. atrox* figured at half natural size by Riggs (1934:17, Fig. 2), the two specimens are virtually identical in every detail.

Apart from size the only difference is in structure of the distal end of the upper canine. In specimens of *T. atrox* the canine is relatively straight throughout its length, while in *N. pattersoni* a distinct lingual bend occurs near the tip. Possibly this feature is a function of age, with the specimens of *T. atrox* representing adults, and the type of *N. pattersoni* a juvenile. The curvature of the distal end of the canine might be functionally advantageous in a young animal, and with age the tips become worn and the tooth attained the linear shape seen in adults. Potential for such a change exists, as the upper canines of thylacosmilids are evergrowing. The size difference between *T. atrox* and *N. pattersoni* might thus be a factor of age. Until more complete specimens of *N. pattersoni* and unquestionable juvenile individuals of *T. atrox* are found this point must remain speculative.

The only other species of thylacosmilid named from the Chapadmalal Formation is *Hyaenodonops chapalmalensis*, known only by its type (MACN 6639), an isolated left M_4. Currently direct comparison of *N. pattersoni* and *H. chapalmalensis* is impossible and conceivably these species might prove synonymous.

In the original description of *N. pattersoni* J. L. Kraglievich (1960) referred a second specimen to this species, MMP S-751, described as a fragment of a right maxilla of a very young individual with DC^1 and apical portion of the erupting C^1. This specimen was collected from level III of the Chapadmalal Formation, Barranca de los Lobos, first point to the northeast of Baliza Caniú, Chapadmalal. MMP S-571 is definitely not a thylacosmilid or even a marsupial; its affinities are not certain. The canines(?) lack both the transverse compression and keel along the outer surface that are characteristic of *Thylacosmilus*. The maxillary(?) is not swollen as occurs in *T. atrox* and the type of *N. pattersoni*. Lastly, deciduous canines are unknown in marsupials.

What features are preserved in MMP S-571 suggest affinities with the Order Carnivora, although more specific identification is not possible at this time. The two canines(?) are oval in cross-section as is typical in living and fossil Carnivora. However, these teeth may not represent DC^1 and C^1, but DI^3 and I^3, or even (but less likely) DC_1 and C_1.

J. L. Kraglievich (1960:64, Fig. 4) described and figured a nearly complete left ulna (MACN 10956) from the Chapadmalal Formation (level IX and X) which he referred to *cf. Notosmilus*. Judging from Kraglievich's description and figure, this bone is similar to elements of *Borhyaena* figured by Sinclair (1906), supporting its borhyaenid or thylacosmilid affinities. Direct comparison of MACN 10956 with unquestionable thylacosmilid ulnae is not yet possible. This specimen might prove referable to *Hyaenodonops chapalmalensis*, the other named thylacosmilid in the Chapadmalal Formation.

Thylacosmilus Riggs, 1933:61

Thylacosmilus Riggs, 1933:61; 1934:3.

Type Species.--*Thylacosmilus atrox* Riggs, 1933:62.

Diagnosis.--Same as for the type and only known species.

Distribution.--Beds of Huayquerian and Montehermosan age; Catamarca and La Pampa Provinces, Argentina.

Thylacosmilus atrox Riggs, 1933:62

(Table 1)

Thylacosmilus atrox Riggs, 1933:62, Fig. 6; 1934:4, Figs. 1-4, Pls. 1-8; Riggs and Patterson, 1939:149; Scott, 1937, Figs. 411, 412; Schultz *et al.*, 1970, Fig. 10; Turnbull, 1976, Figs. 1-5; In press; Zetti, 1972:20-21.
Thylacosmilus lentis Riggs, 1933:62; 1934:5, Pl. 4, figs. 1, 3; Riggs and Patterson, 1939:149.

Type.--FMNH P14531, a nearly complete skull and associated partial skeleton.

Paratype.--FMNH P14344, an associated cranium, mandibular ramus, hind leg, and tarsals.

Referred Specimens.--FMNH P14474 (= MLP 35-X-41-1), a partial skull with dentition. MLP 31-XI-12-4, a nearly complete isolated left upper canine; and MLP 65-VII-29-41, greater part of a right ramus with P_2-M_3 broken and alveoli of M_4, and anterior half of a skull with roots of cheek teeth on right side (this specimen was restored extensively with plaster).

Horizon and Localities.--All FMNH specimens are from Catamarca Province, Argentina. FMNH P14531 and P14474 are from stratum XX of the Corral Quemado Formation at Hualfin near Puerta del Corral Quemado in the Department of Belén; FMNH P14344 is from stratum XIX of the Andalgalá Formation near Chiquimil, Department of Santa María (see Riggs and Patterson, 1939:144 for precise stratigraphic data). These specimens were collected by members of the Second Marshall Field Paleontological Expedition to Catamarca. MLP 31-XI-12-4 is labeled "Araucanense, Catamarca" and was collected by A. Cabrera in 1930.

It is probably from the Andalgalá Formation (= Araucanense) although the exact level of collection is not surely known. MLP 65-VII-29-41 is from the Epecuén Formation, Salinas Grandes de Hidalgo, La Pampa Province, Argentina and was collected by R. Pascual, E. Ortega and E. P. Tonni in 1965.

Age.--Huayquerian and Montehermosan.

Diagnosis.--Large size. Anterior edge of masseteric fossa without deep pit. Talonid small and reduced to tiny posterobasal cuspule on M_4. Anterobasal cingulum absent.

Description.--See Riggs (1933, 1934) for a discussion of the osteology, and Turnbull (1976) for a discussion of the cranial myology.

Measurements.--Table 1. FMNH P14474, L of M^{1-3} = 44.0 mm, L of P^2-M^3 = 63.5 mm; FMNH P14344, L of M_{1-4} = 52.5 mm; FMNH P14531(r), L of M^{1-4} = 59.4 mm, maximum breadth X width of canine at point 100.0 mm from tip of crown = 29.5 X 13.2 mm; MLP 31-XI-12-4, L of canine = 152.0 mm, maximum breadth X width at point 100.0 mm from tip of crown = 31.0 x 10.5 mm; MLP 65-VII-29-41, maximum transverse breadth of condyloid process of jaw = 24.5 mm, depth of ramus below labial side of M_1 = 37.0 mm, same below M_2 = 29.0 mm, same below M_3 - 27.0 mm, L of P_2-M_3 = *ca.* 44.2 mm, L of P_2-M_4 = *ca.* 57.0 mm.

Comments.--Riggs (1933:62) described two species of *Thylacosmilus*. *T. atrox*, the larger, was diagnosed as having a skull length of 260.0 mm, a single toothed P^2, double-rooted P^3, and the frontals not entering into formation of the sagittal crest. *T. lentis* was diagnosed as having a skull length of 197.0 mm, a single-rooted P^2 grooved on its lateral and lingual surfaces, a P^3 with two lateral roots and a vestige of a lingual root, and the frontals entering into formation of the sagittal crest.

The characters used to distinguish these species are of dubious taxonomic value as they possibly represent variations attributable to age and/or sex. Also, it is difficult to explain the presence of two sympatric species displaying virtually identical grades of specialization. As suggested by Zetti (1972:21) all of the specimens of *Thylacosmilus* described by Riggs probably pertain to a single species, and I have considered them as such in this study.

The specimens of *Thylacosmilus* described by Riggs were collected from two distinct horizons in the Province of Catamarca. FMNH P14531 and P14471 are from stratum XX of the Corral Quemado Formation (early? Montehermosan), and FMNH P14344 is from stratum XIX of the Andalgalá Formation (Huayquerian; see Pascual and Odreman Rivas, 1973).

More recently a specimen of *Thylacosmilus* (MLP 65-VII-29-41) was collected from the Epecuén Formation, near Salinas Grandes de Hidalgo, La Pampa Province, Argentina (Pascual and Bocchino, 1963; Zetti, 1972:21). Although this specimen is fragmentary the roots of the upper canine and inflated maxillaries are well preserved. The mandibular ramus is rather complete. As noted by Zetti (1972:21) there are no observable differences between this cranial fragment and the type of *T. atrox*; the same is true for the anterior portion of the mandibular ramus.

Thylacosmilus atrox and *Hyaenodonops chapalmalensis* may be congeneric, although this cannot be determined with the specimens at hand.

DISCUSSION AND CONCLUSIONS

Phylogenetic Relationships.--*Achlysictis* differs from *Thylacosmilus atrox* and *Hyaenodonops chapalmalensis* in its smaller size; presence of a deep pit at the anterior edge of the masseteric fossa (lacking in *T. atrox*, unknown in *H. chapalmalensis*); a proportionately larger talonid cusp on the anterior molars, which is similar in shape and size to the paraconid; proportionately larger talonid cusp on M_4; and the presence of a small anterobasal cingular cusp on the lower molars.

Thylacosmilus atrox (Huayquerian and Montehermosan) and *Hyaenodonops chapalmalensis* (Chapadmalalan) are structurally similar and share the following characters: Size (*H. chapalmalensis* is slightly smaller), paraconid about half the size of protoconid and directly anteriad of that cusp, anterobasal cingular cusp absent, and a small but distinct posterobasal talonid cusp. The nearly perfect agreement in these features suggests that *H. chapalmalensis* might have evolved either directly from *T. atrox* or from a closely related form.

These taxa demonstrate that two distinct lines of evolution occurred within Pliocene Thylacosmilidae. In each line there probably exists an ancestral-descendant relationship between each of the two recognized species. Unfortunately, evolution within each lineage cannot be adequately evaluated with the specimens at hand.

Notosmilus pattersoni (Chapadmalalan) is known from a partial upper canine and associated maxillary fragment, possibly representing a juvenile animal. As the taxonomy of other thylacosmilids is based largely on lower molar morphology, it is not possible to compare *N. pattersoni* with all other known taxa. *N. pattersoni* might prove synonymous with *Hyaenodonops chapalmalensis*. It is equally possible, although unlikely, that *N. pattersoni* might have affinities with *Achlysictis*, while *Hyaenodonops* could prove referable to *Thylacosmilus*.

If *Notosmilus pattersoni* and *Hyaenodonops chapalmalensis* are truly distinct, then their presence in the same beds marks the only known sympatric occurrence of two species of Thylacosmilidae. Such being the case it is difficult to explain the sympatric occurrence of two species displaying virtually identical and unique feeding specializations.

Origin of the Thylacosmilidae.--Thylacosmilids are known from beds of Huayquerian through Chapadmalalan (Pliocene) age in Argentina. When thylacosmilids first appear in the fossil record they are already highly specialized, indicating that there is probably a long unknown history of this family.

Scott (1937:71) suggested that the Casamayoran (early Eocene) borhyaenid *Arminiheringia* might be ancestral to *Thylacosmilus*. Simpson (1948:42) pointed out that the vast gap between these two forms might allow for such a transformation, although there is little positive evidence to favor such a relationship. The enlargement of both upper and lower canines and the shallow rather than flanged symphysis of *Arminiheringia* hardly suggest beginnings of saber-tooth specializations.

Despite these differences, many specializations of *Arminiheringia* foreshadow those seen in *Thylacosmilus*. These include: Reduction in size of metaconid and talonid on lower molars, virtual absence of a protocone, reduction in size of anterior two premolars, reduction of lower incisors to two in each jaw, and large and apparently open rooted canines in adults. In these features *Arminiheringia* is the most thylacosmilid-like of known borhyaenids, although this does not necessarily imply a direct phylogenetic relationship between the two.

Functional Significance of the Thylacosmilid Saber-tooth.--A possible parallel for the apparent similarities between *Arminiheringia* and Pliocene thylacosmilids is found in North American Tertiary saber-tooth groups. In the Eocene occurs the saber-tooth creodont *Apataelurus* (see Scott, 1938), and in the later Tertiary the widespread saber-tooth machairodontine cats (*e.g.*, *Homotherium*, *Smilodon*) (Thenius, 1967, Fig. 1). The saber-tooth creodont *Apataelurus* and saber-tooth machairodontine cats had distinct histories having evolved from different ancestral forms. *Apataelurus* can be considered successful during its time, although it was far less specialized than the machairodonts which evolved later.

By analogy it is reasonable to postulate that *Arminiheringia*, like *Apataelurus*, represents an early Eocene experiment in development of large canines, while the Thylacosmilidae, like Machairodontinae, evolved independently, appeared later in the fossil record, and achieved greater saber-tooth specialization.

Development of saber-like upper canines with complementary bony flanges on the lower jaw to protect these teeth, has evolved independently in various groups of flesh-eating mammals. In the South American Pliocene thylacosmilids, in the North American Eocene creodont *Apataelurus*, and three or more times in the Felidae (Oligocene through Pleistocene) (see Thenius, 1967, Fig. 1).

The independent evolution of the saber-like upper canines in several lineages of carnivorous mammals has stimulated speculation as to their function. Absence of close recent analogues has furthermore made inferences difficult. It is thus not surprising that a large literature has accumulated on this subject and that strong differences of opinion exist (Simpson, 1941:1).

Some early interpretations of the feeding habits of saber-tooth carnivores include blood sucking (Merriam and Stock, 1932), carrion feeding or scavenging (Bohlin, 1940; Marinelli, 1938; Weber, 1904), use of the saber-like canines to slice meat before ingestion (Marinelli, 1924, 1938), and Bohlin (1940) suggested their use for shoveling masses of sliced meat into the mouth. Miller (1969) recently suggested that *Smilodon* was able to use the incisors either in conjunction with or independently of the upper canines; the animal being capable of ingesting meat in a manner similar to other carnivores, such as canids. It must be noted that *Thylacosmilus* has no incisors, so some of the conclusions reached by Miller for *Smilodon* are not applicable to thylacosmilids.

It is now generally agreed that saber-tooth carnivores were predaceous and the canines used for stabbing (transfixing) and/or slicing (cutting and tearing) (Simpson, 1941:1). The stabbing theory was first proposed by Warren (1853) and more explicitly developed by Brandes (1900). The arguments presented by the latter author were weakened by the suggestion of adaptation for preying on glyptodonts. As pointed out by Simpson (1941:1) the armor of glyptodonts and canines of the machairodont cats were fully developed millions of years before these two sorts of animals ever came into contact. Even if we consider the contemporaneous occurrence of thylacosmilids and glyptodonts within South America, there is no compelling evidence for coevolution of these forms. Furthermore, it is impossible to conceive use of the saber-like canines of *Thylacosmilus* to pierce the thick carapace of large glyptodonts in which bone attained a thickness in excess of 30-40 mm.

The most widely accepted theory, first proposed by Matthew (1901, 1910), is that the usual prey of saber-tooths were the thick-skinned ungulates (pachyderms), the action being to strike and then rip or gash so that the prey bled to death (Simpson, 1941). Bohlin (1940) later rejected the stabbing theory entirely and maintained that the sabers were ill-adapted for this function and must have served mainly or wholly for slicing.

By a careful consideration of the mechanical nature of the canines and analysis of motion of the head, Simpson (1941) presents a convincing and reasonable interpretation of saber-tooth habit and function. Simpson's conclusions are as follows:

1) Stabbing was primarily correlated with the differentiation of the saber canines from "normal" canines and therefore is the principal functional element in the saber-tooth specialization.

2) Saber-like canines are ill-adapted for slicing, but doubtless could be and were used to make a short slice or gash. This function is considered secondary and the stabbing primary. Pure stabbing and down-and-up slicing seem to be the norms of the two most likely uses of the canines. Kurtén (1968) has distinguished those placental saber-tooths that mostly stab as the dirk-toothed forms, from those that stab and then mostly slash as the scimitar-toothed forms.

3) This primary adaptation of the canines and the general body structure are more consistent with predaceous habits than with carrion eating. The evidence seems to favor the usual view that these animals were primarily predators.

4) The animal did not have to come to a full stop before it started the stabbing motion. Forward attack was a useful preliminary phase of stabbing and contact with the prey animal coincided with the strongest stabbing momentum.

5) The saber-tooths could cling to the back of an animal with their powerful front limbs which were proportionately larger than the hind limbs and well adapted for grasping prey. These front legs would themselves be powerful weapons and they could have served to deliver the *coup de grace* to an animal slowed or stopped by the canine stab.

6) The powerful fore-limbs and long canines might possibly be considered coordinated parts of a dual apparatus for killing prey.

It is probable, as noted by Riggs (1934:30), that the habits of thylacosmilids and their method of killing prey were similar to that of machairodontine saber-tooths. *Thylacosmilus* had a relatively short and stout humerus with a massive deltoid crest, a strong supinator ridge and a small internal condyle (Riggs, 1934:25). The humerus shares the general characters of crouching animals hunting from ambush as distinguished from cursorial, in the sturdiness of the bone as a whole and in the great length of the deltoid crest and supinator ridge. The fore-limb of *Thylacosmilus* was unusually powerful compared with the hind-limb, and may have been used for grasping prey as in machairodontine cats.

Turnbull (In press) notes that *Thylacosmilus* had a greater degree of specialization for one or more of the aspects of the sabertooth way of life than for its placental counterparts. *Thylacosmilus* "...apparently became so proficient at both stabbing and slashing that it in effect combined the dirk and the scimitar-toothed specialties, and in so doing it was able to abandon its incisors and their related function." "Hence...[*Thylacosmilus*]...is not only remarkably parallel to the placental saber-toothed forms, but has its own unique specialized varient of that way of life."

Schultz *et al.* (1970:22) pointed out the extraordinarily close similarity between the North American machairodontine cat *Barbourofelis* and the South American *Thylacosmilus*, noting that these animals represent an excellent example of convergence in evolution. They suggest, however, that these animals could not have been similar in the way they stabbed. According to their argument, in *Barbourofelis* the elongated canines are parallel and were probably imbedded simultaneously in the animal's prey. In *Thylacosmilus* the upper canines diverge ventrally (reference made to Riggs, 1934, Pl. 3, fig. 1) and they could not have been imbedded at the same time without being spread apart. They note that the canine blade in *Thylacosmilus* is triangular in cross-section, being strengthened by a median ridge on its labial side. This, they note, is suggestive of the canines of some peccaries, and indicates that the canines may have been used to slash laterally as is the case in many living pigs. *Barbourofelis*, they conclude, seemed to have been a purely stabbing cat whose canines were too long and poorly serrated to have been effective slashing weapons.

I strongly oppose the view that *Thylacosmilus* might have used its canines to slash laterally by analogy with living pigs. In the first place the upper canines of *Thylacosmilus* are deeply rooted in the maxillary and extend to a position well above and between the orbits. By being well braced, there is little reason to assume that these teeth would spread when imbedded in the prey. Moreover, the degree of divergence of the canines in the type of *Thylacosmilus* is not as extensive as shown in Riggs' figure and hence is somewhat erroneous (Turnbull, In press).

Secondly, as noted by Simpson (1941:10), the tusks of pigs and of some extinct forms like South American astrapotheres, are so unlike the sabers here under discussion as to prove little basis for inference.

Thirdly, there would be a preponderance of strain at the alveolus and on the blade in any direction other than along the tooth axis (Simpson, 1941:8). The tooth blade is relatively thin transversely and excess lateral strain would likely result in breakage. It is probably for this very reason that the mandibular flange evolved to protect the upper canine from such forces and possible damage when the mouth was closed. It would thus be advantageous for the animal to restrict movement of the canine to a direction in which existed the least potential for strain, this being along the tooth axis and hence in an anteroposterior direction.

Turnbull (1976:154) further notes that the head-controlling musculature of *Thylacosmilus* must have been not only extremely powerful, but also superbly capable of manoeuvering the head and its attached canine blades with great precision. "Otherwise there would be risk of an angled or transverse blow resulting in breakage of the greatly elongated and unprotected canines." "That the canines themselves must have been quite vulnerable to damage from a forceful lateral blow is indicated by their cross-section which is thin mediolaterally and by the presence of a full-length symphyseal "scabbard" or "sheath"."

Simpson (1941:11) noted that continuous replacement of the saber-like canines as comparable to fang replacement in snakes, would be advantageous in saber-tooth carnivores. Polyphyodontism, however, is extremely rare in mammals and is not found in any saber-toothed group. The saber-tooth machairodontines did have well developed and long-functioning deciduous canines, which was about as far in this direction as machairodontines came to solving the problem.

Deciduous canines are unknown in thylacosmilids, as in all Marsupialia, yet the group has dealt with possible canine breakage by employing a different strategy. The presence of evergrowing canines allowed for restoration and functional replacement of the teeth should they be broken. By such a mechanism a broken tooth would only temporarily hinder the normal activities of an animal. Bohlin's (1940) suggestion that animals with broken sabers depended on carrion seems reasonable.

Prey and Extinction.--Accepting that thylacosmilids, as did *Smilodon*, fed upon large thick-skinned pachyderms, there was certainly a plentiful food supply during Pliocene times in South America. Included are two families of large ground sloths (Mylodontidae and Megatheriidae, Order Edentata), the rhinoceros-like Toxodontidae (Order Notoungulata), and possibly the camel-like Macraucheniidae (Order Litopterna). All of these groups have fossil records extending well back into the early part of the mid-Tertiary. It is conceivable that with evolution and increase in size of these forms there occurred coevolution and increased specialization of the Thylacosmilidae. It must be stressed, however, that the fossil record is not clear on this point.

Practically all knowledge of early to mid-Tertiary (Paleocene-Miocene) South American vertebrate faunas is from the southern part of that continent and largely from Argentina. Thylacosmilids make their first appearance in the fossil record in Pliocene beds in the northern part of Argentina. In speculation, thylacosmilids might have evolved in the northern part of Argentina or more generally in the central part of the South American continent, possibly in the mid-Tertiary. This would explain their absence in mid-Tertiary faunas in southern South America and their first appearance at a more northern locality.

Thylacosmilids make their last appearance in the Chapadmalal Formation (latest Pliocene), near Mar del Plata, Buenos Aires Province, Argentina. At about this same time the panamanian land-bridge came into existence connecting North and South America. With the appearance of this bridge the long isolation of the South American continent ended. A permanent dispersal route was at last open for overland migration and a spectacular interchange of the two continental faunas began (Patterson and Pascual, 1972:284).

In beds of Uquian (earliest Pleistocene) age, which immediately overlie the Chapadmalal Formation, placental saber-tooth machairodontine cats appear for the first time in the fossil record of South America. The generic and specific status of this oldest known allochthonous South American saber-tooth felid is disputed. J. L. Kraglievich (1948) originally named it *Smilodontidion riggi*. Churcher (1967:256) considered this species a small form of *Smilodon*, and synonymized it with *Smilodon neogaeus*, which he recognized as the only species of *Smilodon* in the Pleistocene of Argentina. It is pointed out by Patterson and Pascual (1972:289) that if this generic identification is correct this is an earlier record for the genus than any in North America. They further suggest the possibility that *Smilodontidion* may actually be *Megantereon*. In addition, *Smilodon popular* is the species usually called *S. neogaeus*. *"Hyaena" neogaea* Lund is, however, a *nomen nudum* (Paula Couto, 1955).

The important point to remember for this study is that placental saber-tooths first appear in the South American fossil record in beds of Uquian age and continue into and through beds of Lujanian (latest Pleistocene) age. The last appearance of marsupial saber-tooths and the first appearance of placental saber-tooths in immediately overlying beds, between which there was but a short time lapse as inferred from faunal studies, suggests the replacement of marsupial saber-tooths by immigrant placental saber-tooths. Similar "ecological replacement" of other established South American inhabitants by North American immigrant groups at this same time is well documented. No better example of a geologically sudden meeting of two radically different faunas and of the ensuing consequences exists in the geological record (Patterson and Pascual, 1972:284).

There is little doubt that the appearance in South America of placental saber-tooths marked the fate of thylacosmilids. Within a very short period of time, geologically speaking, thylacosmilids underwent a rapid decline to extinction. The reign of the most specialized and bizarre group of large predaceous marsupials yet known ended.

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A REVIEW OF PALEOCENE AND EOCENE LEPTICTIDAE (EUTHERIA: MAMMALIA) FROM NORTH AMERICA

by

MICHAEL J. NOVACEK[1]

ABSTRACT

Abundant and widely distributed fossils demonstrate a diversity of leptictid species in North America during the Paleocene and Eocene epochs. The late Cretaceous genus *Gypsonictops* markedly contrasts with the Tertiary leptictids, but is recognized as the most closely related sister taxon of the latter. The genus *Diacodon* is removed from the Leptictidae because the type species, *D. alticuspis*, more closely resembles adapisoricid insectivores. Three major leptictid lineages are known from the Paleocene and Eocene of North America. One lineage, the genus *Prodiacodon*, shows the retention of primitive sectorial features in the dentition. The second lineage, *Palaeictops*, shows a more derived "bunodont" condition. *Palaeictops*, particularly *P. matthewi* (n. sp.), is undoubtedly closely related to the Oligocene *Leptictis*. *Myrmecoboides* represents the third early divergent lineage not closely related with other leptictid genera. A new species, *Prodiacodon crustulum*, from the Puercan of Montana shows a combination of dental characters intermediate between *Gypsonictops (Hypoconus)* and *Prodiacodon puercensis*.

INTRODUCTION

The Leptictidae is an archaic family of eutherian mammals with a long evolutionary history. Earliest undoubted members are known from the early Paleocene of North America and the family persisted with reasonable diversity until the end of the middle Oligocene. Records of the group in Europe are fewer with cited occurrences from the later Paleocene of Germany (Russell, 1964), the middle Eocene of Germany (Tobien, 1962) and the late Eocene or early Oligocene of France (Filhol, 1892).

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The primitive nature of the Leptictidae has long been recognized and the family has been cited as a central stock from which a number of important eutherian groups might be derived (Lillegraven, 1969; Clemens, 1973). Others (Szalay, 1968; Clemens, 1974) have concluded that leptictids were not direct ancestors of such groups as primates. Leptictids have been included in the Order Insectivora in many classifications (e.g., Simpson, 1945; Van Valen, 1967). However, as Butler (1956, 1972) and McDowell (1958 and unpublished studies) have pointed out, the family does not share with undoubted insectivores such specializations as a loss of a medial internal carotid artery, the absence of the entotympanic as a bullar component, the crowding out of palatine by the maxillary bone in the orbital region of the skull, and the loss or reduction of a jugal bone. Accordingly, Butler (1972) has proposed the recognition of the order Proteutheria from Romer's (1966) suborder and the inclusion of the Leptictidae within it. Butler (1972) acknowledged that his establishment of the Proteutheria was a matter of practicality. The majority of similarities between members of this group merely represent shared-primitive eutherian characters. Thus the order replaces the Insectivora as a "waste-basket" category. More recently, McKenna (1975) has proposed that Tertiary leptictids belong to the superorder Leptictida also comprising anagalids, macroscelidids, and lagomorphs. Other members of Butler's Proteutheria were relegated by McKenna to various eutherian "supergroups". McKenna's Leptictida is a stimulating concept, in part suggested by evidence from the skull, dentition, and postcranial skeleton. Nevertheless this idea has yet to be tested rigorously with a careful analysis of the available morphological evidence. Such a critique is not the subject of this review, and, in recognition of the current controversy on the matter, I have not formally assigned leptictids to any of proposed higher categories. An assignment will be made following a detailed study of the broader affinities of the Leptictidae (Novacek, unpublished data). The aims of the present paper are confined to a characterization of the family and taxonomic revision of its Paleocene and Eocene members.

DISTRIBUTION

Fig. 1 shows the localities where North American Paleocene and Eocene leptictids described in this report have been recovered. The figure is accompanied by Table 1 listing the land mammal age, formation, and leptictid taxa represented at a particular locality. It is evident that leptictids had a widespread distribution throughout much of the Rocky Mountain region of western North America during early Cenozoic times.

METHODS

The dental nomenclature employed here follows that of Rich (1971: 4).

All specimens were measured on an Ehrenreich Photo Optical "shopscope." Measurements were in millimeters and were rounded off to

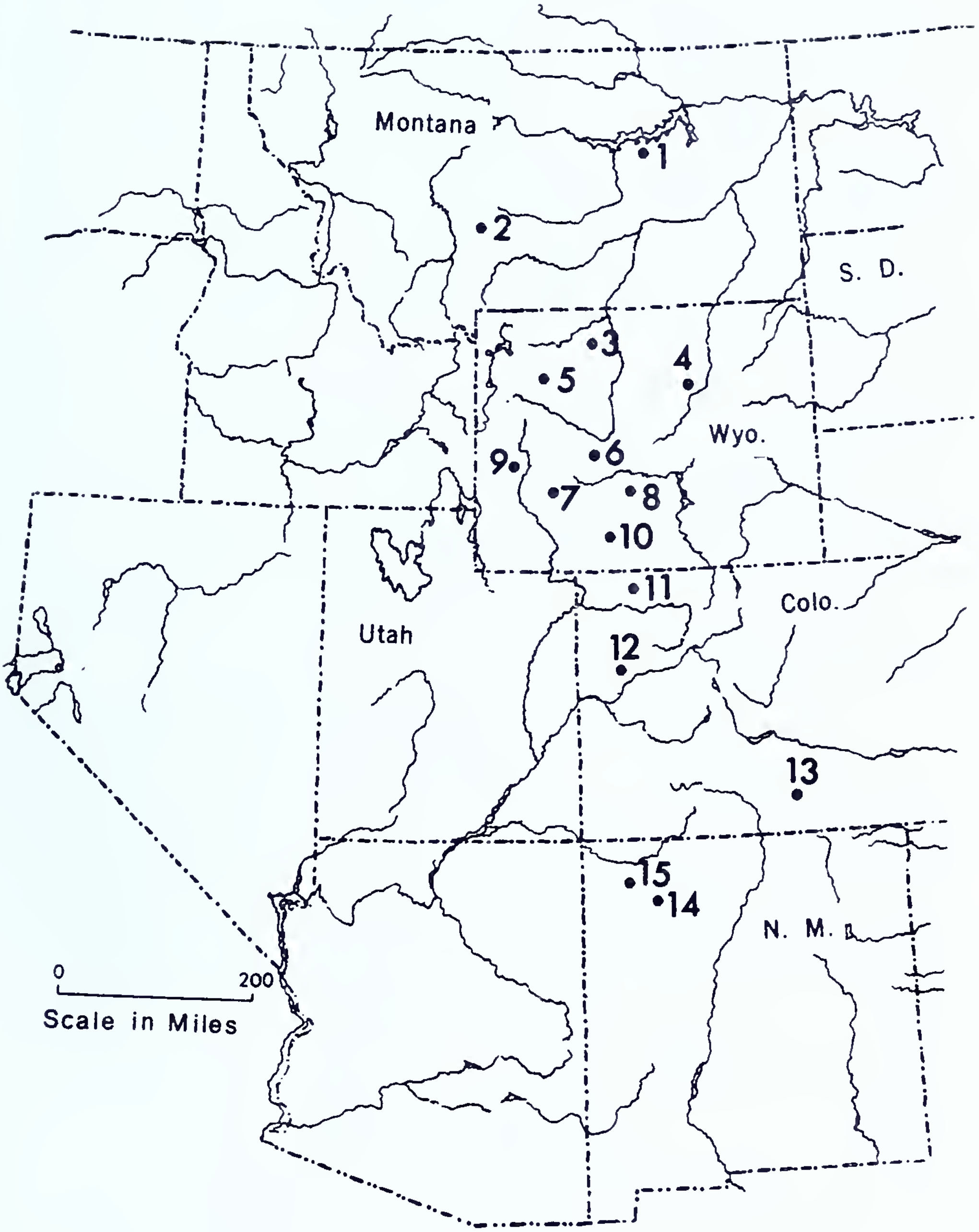

FIG. 1. Map showing Paleocene and Eocene North American localities where leptictids described in this report have been recovered. Numbers refer to localities listed in Table 1.

TABLE 1. North American Paleocene and Eocene localities where leptictids described in this report have been recovered.

Locality	Age	Formation	Taxa
1. Garbani	Puercan	Tullock	*Prodiacodon crustulum*
2. Crazy Mtn. Field, Gidley Quarry	Torrejonian	Fort Union	*Myrmecoboides montanensis* *Prodiacodon concordiarcensis* *Prodiacodon furor*
3. Bighorn Basin	Wasatchian	Willwood	*Prodiacodon tauricinerei* *Palaeictops bicuspis*
4. Powder River	Wasatchian	"Wasatch"	*Prodiacodon tauricinerei*
5. Tepee Trail	Uintan	Tepee Trail	*Palaeictops sp.*
6. Wind River Basin, Bridger Creek	Wasatchian	Wind River	*Palaeictops bicuspis* *Palaeictops multicuspis* *Prodiacodon tauricinerei*
7. Tabernacle Butte	Bridgerian	Bridger	*Palaeictops bridgeri*
8. Bison Basin	Tiffanian	Fort Union	*Prodiacodon concordiarcensis*
9. Big Piney	Wasatchian	Wasatch	*Prodiacodon tauricinerei*
10. Bitter Creek	Wasatchian	Wasatch	*Prodiacodon tauricinerei*
11. Four Mile, East Alheit Pocket	Wasatchian	Wasatch	*Prodiacodon tauricinerei*
12. Cherard Park	Wasatchian	Wasatch	*Palaeictops matthewi*
13. Garcia Canon	Wasatchian	Huerfano	*Palaeictops matthewi*
14. Arroyo Blanco	Wasatchian	San Jose	*Prodiacodon tauricinerei*
15. San Juan Basin, Torrejon Arroyo	Torrejonian	Nacimiento	*Prodiacodon puercensis*

the nearest one-hundredth of a millimeter. The following orientation for measuring cheek teeth (Fig. 2) were used in this report.

ANTEROPOSTERIOR AXIS ("A-P") AXIS

Lower posterior premolars - long axis of tooth.
Lower molars - line drawn through the apices of the metaconid and the entoconid.
Upper posterior premolars - line extended from anteriormost point of the anterolabial lobe to the posteriormost point of the metastylar lobe.
Upper molars (M^{1-2}) - line drawn through the apices of the paracone and metacone.
Upper molars (M^3) - line drawn at right angles to a line which divides the tooth into equal anterior and posterior halves.

LENGTH

Lower posterior premolars - total length of crown, i.e., greatest dimension measured parallel to "A-P" axis.
Lower molars - total distance from the anterior face of the paraconid to the back of the talonid along a line parallel to the "A-P" axis (anterior cingulum not included in measurement).
Upper posterior premolars and upper molars - greatest dimension parallel to the "A-P" axis of tooth.

WIDTH

Lower posterior premolars - widest part of crown; greatest dimension measured at right angles to "A-P" axis.
Lower molars - two width measurements: *trigonid width*, *talonid width*, widest part of each of these sections of the crown measured at right angles to "A-P" axis.
Upper posterior premolars and upper molars - two measurements *anterior width*, distance from the labialmost point of the anterolabial corner of the crown to the lingualmost point of the protocone; *posterior width*, distance from posterolabialmost point of metastylar lobe to lingualmost point of protocone, both width measurements taken at right angles to the "A-P" axis.

The dental measurements of all specimens studied are given in Table 2.

ABBREVIATIONS

AMNH - American Museum of Natural History
CMNH - Chicago (Field Museum) of Natural History
LACM - Los Angeles County Museum
PU - Princeton University
UCMP - University of California Museum of Paleontology
CIT - California Institute of Technology

DENTAL IDENTIFICATIONS

The primitive eutherian dental formula is traditionally recognized as $I\frac{3}{3}C\frac{1}{1}P\frac{4}{4}M\frac{3}{3}$. McKenna (1975) has proposed a novel hypothesis of dental evolution in the Eutheria, maintaining that the

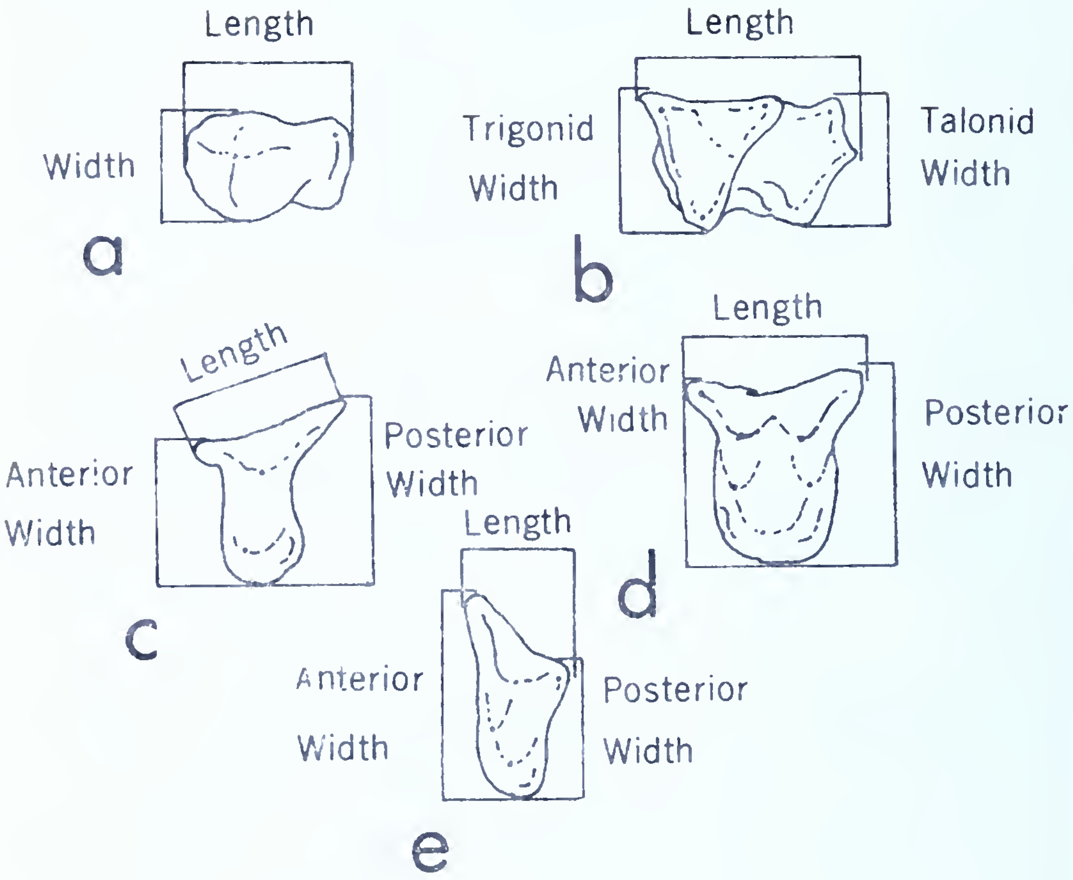

FIG. 2. Diagram showing criteria for dental measurements of a) lower posterior premolars, b) lower molars, c) upper posterior premolars, d) upper molars, and e) upper last molar (M^3). See text for explanation.

most primitive members of the infraclass had 5 upper and lower premolars. He identifies the dental formula in these forms as $I\frac{1}{1}I\frac{2}{2}I\frac{3}{3}C\frac{1}{1}P\frac{1}{1}P\frac{2}{2}P\frac{3}{3}P\frac{4}{4}P\frac{5}{5}M\frac{1}{1}M\frac{2}{2}M\frac{3}{3}$. There is evidence that a (unknown) lineage which gave rise to Tertiary leptictids had such a dental formula. Lillegraven (1969, p. 57) and Clemens (1973, p. 6) described specimens of the late Cretaceous genus *Gysonictops* with five lower premolar loci, reduction to four in number occurring through loss of the reduced tooth at the third premolar locus (P_c of Clemens' and Lillegraven's notation) in at least one known specimen. In all Tertiary leptictids where a complete dental row is known, only four premolars are present. McKenna (1975) identifies these as $P\frac{1}{1}P\frac{2}{2}P\frac{4}{4}P\frac{5}{5}$, arguing that $P\frac{3}{3}$ (and, or $DP\frac{3}{3}$) were lost in leptictids. It is recognized in this study that *Gypsonictops* is closely related to Tertiary leptictids. McKenna's dental hypothesis is thus more compatible with this phylogenetic picture than traditional dental designations. In this paper $P\frac{5}{5}$ = tradi-

TABLE 2. Measurements of cheek teeth of North American Paleocene and Eocene leptictids described in this report. All measurements are in millimeters.

	Upper Cheek Teeth				Lower Cheek Teeth		
Element	Length	Anterior Width	Posterior Width	Element	Length	Trigonid Width	Talonid Width
AMNH 4802 Type of *Palaeictops bicuspis*							
LP^4	5.25	2.80		LP_5	3.92	1.55	2.14
LP^5	3.40	4.40	3.86	LM_1	3.11	2.15	2.35
LM^1	3.07	3.81	4.11	LM_2	3.00		
LM^2	2.72	3.97	3.75	LM_3	3.27	2.37	1.70
LM^3	2.44	3.17	2.65				
				AMNH 4255			
				LM_2	3.09	2.00	2.45
				LM_3	3.40	2.30	2.14
Palaeictops bridgeri							
				AMNH 56032 Type			
				RP_5	4.25	2.31	2.22
				RM_1	3.65	2.53	2.47
				RM_2	3.58	2.69	2.64
				RM_3	4.00	2.39	2.03
Palaeictops multicuspis							
				AMNH 14741 Type			
				LP_2	3.66	1.42	
				LP_4	4.42	1.74	
				LP_5	4.21	2.41	2.21
				LM_1	3.20	2.67	2.63
				LM_2	3.27	2.65	2.47
				LM_3	3.40	2.50	2.09
Palaeictops matthewi							
CMNH 26904 Type							
RP^4	3.26	2.50		LP_4	4.02	1.60	
RP^5	2.80	3.21	3.56	LP_5	3.90	2.05	1.84
RM^1	2.90	4.03	4.17	RM_1	3.10	2.36	2.04
RM^2	2.82	4.41	4.16	RM_2	3.21	2.36	2.13
RM^3		3.60					
CMNH 26481							
RP^4	3.57	3.06					

TABLE 2. Continued.

	Upper Cheek Teeth				Lower Cheek Teeth		
Element	Length	Anterior Width	Posterior Width	Element	Length	Trigonid Width	Talonid Width
Myrmecoboides montanensis							
				USNM 8037 Type			
				LP_5	2.95	1.46	1.12
				LM_1	2.37	1.63	1.40
				LM_2	2.42	1.65	1.40
				LM_3	2.67	1.75	1.35
Prodiacodon puercensis							
AMNH 16011 Type							
RP^5	2.62	4.00	4.40				
AMNH 16748							
RP^4	3.50	3.03		LP_5	3.90	2.13	2.04
RP^5	3.31	3.87	4.28	LM_1	3.45	2.80	2.56
RM^1	3.15	4.67	5.14	LM_2	3.48	3.13	2.36
RM^2	3.40	5.15	5.33	LM_3	3.80	2.81	1.93
RM^3	2.33	4.14	3.67				
Prodiacodon tauricinerei							
PU 13104 Type							
LP^4	2.75	2.39		RP_4	2.96	1.41	
LP^5	2.10	3.25	2.95	RP_5	3.10	1.65	1.59
LM^1	2.65	3.48	3.53	RM_1	2.39	1.83	1.72
LM^2	2.66	3.99	3.85	RM_2	2.46	1.92	1.77
				RM_3	2.77	1.70	1.30
PU 14726							
				AMNH 80695			
LP^4	3.01	2.11					
LP^5	2.81	2.87	3.01	LP_5	3.06	1.53	1.47
LM^1	2.65	3.23	3.27	LM_3	2.53	1.75	1.39
LM^2	2.34	3.82	3.55				
LM^3	2.10	3.40	2.71				

TABLE 2. Continued.

Element	Lower Cheek Teeth Length	Trigonid Width	Talonid Width	Element	Lower Cheek Teeth Length	Trigonid Width	Talonid Width
Prodiacodon tauricinerei							
				AMNH 48763			
AMNH 80023				LP_5	3.09	1.22	1.56
				LM_1	2.42	1.85	1.63
RP_5	2.96	1.65	1.51				
RM_1	2.97	1.97	1.22	USNM 19204			
RM_2	2.41	2.52	1.85				
RM_3	2.82	1.95	1.51	LM_2	2.72	2.25	1.91
Prodiacodon concordiarcensis				LM_3	2.94	2.07	2.57
USNM 9637 Type				USNM 35693			
LP_5	2.14	1.29	1.02	RM_1	2.06	1.45	1.29
LM_3	1.95	1.43	1.47	RM_2	1.83	1.51	1.13
				RM_3	1.89	1.40	1.00
USNM 20970							
LP_5	2.40	1.67	1.25				
LM_1	2.15	1.85	1.40				
Prodiacodon furor							
AMNH 35291 Type				AMNH 35289			
RP_5	3.09	1.68	1.40	LP_5	2.39	1.57	1.20
				LM_1	2.29	2.00	1.13
AMNH 35290				LM_2	2.16	1.82	1.45
RM_1	2.54	1.91	1.73				
RM_2	2.52	1.98	1.62				

Element	Upper Cheek Teeth Length	Anterior Width	Posterior Width				
Prodiacodon crustulum							
UCMP 114990				UCMP 114993			
LM^1	2.4 *	4.0 *	4.08 (Type)	DP_5	3.74	1.47	1.44

TABLE 2. Continued.

Element	Upper Cheek Teeth Length	Anterior Width	Posterior Width	Element	Lower Cheek Teeth Length	Trigonid Width	Talonid Width
Prodiacodon crustulum							
LACM 32970				UCMP 114991			
RM^1	2.67	3.75	3.82	LM_1 or $_2$	2.81	2.25	1.83
UCMP 114980				UCMP 114985			
LM^x	2.40	3.99	3.9 *	LM_3	3.27	1.79	1.57
UCMP 114976				UCMP 114992			
RM^x			3.99	LM_1?	2.84	2.04	1.72
UCMP 114979				UCMP 114981			
LP^4	3.45	2.21		LM_2?	2.74	1.94	1.80
UCMP 114974				UCMP 114986			
LP^4	3.19	2.23		RM_2?	2.91	2.09	1.79
UCMP 114972							
LP^5?	2.58	3.14	3.38				

* Tooth damaged, measurement approximate
^{x} Position in tooth row unknown

tional $P\frac{4}{4}$, $P\frac{4}{4}$ = traditional $P\frac{3}{3}$, and $P\frac{3}{3}$ are thought to be absent. All other dental identifications correspond to their traditional designations. $P\frac{1}{1}$ may actually be $DP\frac{1}{1}$ as there is no evidence of replacement at this locus in primitive eutherians.

SYSTEMATIC PALEONTOLOGY

Family LEPTICTIDAE Gill, 1872

Diagnosis.-- Dental formula $I\frac{2}{3-2}C\frac{1}{1}P\frac{1}{1}$ (or $DP\frac{1}{1}$) $P\frac{2}{2}P\frac{4}{4}P\frac{5}{5}M\frac{1-3}{1-3}$. Canines and (D)$P\frac{1}{1}$ single rooted. P_4 double rooted, usually trenchant without a basined talonid. P_5 molariform with paraconid and basined talonid with three or more cusps. Molar trigonids anteroposteriorly compressed. Molar talonids with large shallow basins. Entoconulid often present. M_3 with salient hypoconulid. P^4 with paracone, metacone, protocone (protocone secondarily lost in *Leptictis haydeni*) anterior accessory cuspule, and posterior cingulum. Molariform P^5 (hypocone reduced, vestigial, or absent in some forms) with posterior and anterior cingula. Upper molars with labially positioned paracone and metacone, very narrow ectocingulum, paraconule and metaconule, pre- and postcingula and a hypocone. Skull (where known) with elongate snout, elongate nasal bones, and small lacrimal foramen. Infraorbital canal short. Jugal bone present. True postglenoid process well developed. Subsquamosal foramen present. Maxilla with large orbital wing. Auditory bulla formed by entotympanic bone, not completely covering tympanic cavity. Medial branch of the internal carotid artery present, but small. Flange of the periotic at the posterior wall of tympanic chamber absent and the fenestra rotunda fully exposed. Stylomastoid foramen not isolated from the tympanic chamber by the tympanohyal. All known leptictid skeletons have the following diagnostic features: Forelimb much shorter than hindlimb. Enlarged deltoid crest present on anterior surface of humerus. Hindlimb with elongate tibia, fibula, and pes. Tibia-fibula contact broad or bones fused distally. Sternum enlarged with prominent keel. Strong pubic symphysis. Astragalar foramen present ventrally, but not dorsally. Elongate metatarsals and phalanges. Plantigrade.

Age and Distribution.-- Early Paleocene - late Oligocene, North America; late Paleocene-?late Eocene, Europe (see Fig. 1, Table 1 for distribution of North American Eocene and Paleocene leptictids).

Genera excluded.-*Diacodon* (type *D. alticuspis*) has long been considered a leptictid. The type specimen of *D. alticuspis*, USNM 1098 from San Jose Formation, New Mexico, (See Cope, 1875, Matthew and Granger, 1918), a very poorly preserved lower jaw, has a broken last premolar which is uncharacteristically submolariform. Excellent undescribed cranial and dental material of *Diacodon alticuspis* from the San Jose Formation further demonstrates that this species is not a leptictid. *Diacodon alticuspis* differs from leptictids in having 1) a last premolar with a small metaconid, a paraconid that does not project far anteriorly, and a very shortened talonid with only one or two cusps; 2) lower molars with low trigonids which lean slightly forward toward their apices, a very low cristiform paraconid, a reduced, centrally positioned hypoconulid, and a hypoconid that is worn flat and much lower than the entoconid; 3) a penultimate upper premolar that is minute relative to the last one and has only one main cusp; 4) a last upper premolar that is submolariform, lacking a definite hypocone and having a small metacone on the posterior shoulder of the paracone, a strong postmetacrista leading to the posterolingual corner of the crown, and a protocone much lower than the paracone and metacone; 5) upper molars that are not transverse but anteroposteriorly broad with prominent parastylar and metastylar lobes, and strong postmetacristae. In these features *D. alticuspis* more closely resembles adapisoricids and the similarity of this species to *Scenopagus edenensis* (Robinson, 1966) and *S. mcgrewi* (McKenna and Simpson, 1959) is striking.

Other species of *Diacodon* have either been removed from the Leptictidae (see Robinson, 1966, and Van Valen, 1967) or referred to other leptictid genera (see below).

Leptonysson basiliscus Van Valen (1967) from the medial Paleocene (Torrejonian) Crazy Mountain Field Fauna of Montana is here excluded from the Leptictidae in agreement with arguments presented by Clemens (1973, p. 29-30). *Diacodon packi* (originally described as *Leptacodon packi* by Jepsen, 1930a) has a submolariform last lower premolar and is probably a nyctitheriid related to *Leptacodon tener* (McKenna, 1968).

Remarks.-- The most recent review of the Leptictidae was published by Van Valen (1967) who subdivided the family into three subfamilies - Procerberinae, Gypsonictopinae and Leptictinae. The Gysonictopinae includes only the late Cretaceous genus *Gypsonictops*, whose reference to the Leptictidae has been questioned (Butler, 1972). Clemens (1973) considered the relationship of *Gypsonictops* in detail and referred this genus to the Leptictidae but pointed out such action requires a substantially broader definition of the family. Unlike all Cenozoic leptictids, *Gypsonictops* variably has 5 lower premolars set closely in the jaw, the paraconid of $P_{\overline{5}}$ is small or absent, and the $P^{\underline{5}}$ and upper molars usually lack distinct hypocones. In all specimens where the posterior region of the mandible is preserved an inflected angular process is present. The ectocingulum or stylar shelf on the upper molars is much broader than that in Cenozoic leptictids. Lillegraven (1969, p. 58) and Clemens (1973, p. 33) have also remarked on the significant difference in occlusal pattern between *Gypsonictops* and other leptictids. Since four upper and lower premolars, a molariform $P_{\overline{5}}$, and molar hypocones are key diagnostic characters of all leptictids excepting *Gypsonictops*, strong argument is provided for removing the latter from the family. It presently seems best to regard *Gypsonictops* as the most closely related sister group but not as a definite member of the Leptictidae. The possible relationships of *Gypsonictops* with other eutherian families has been considered at length by Szalay (1968), Lillegraven (1969), Clemens (1973) and McKenna (1975).

Van Valen's (1967) leptictid subfamily Procerberinae has been shown by Lillegraven (1969) to be more properly allied with *Cimolestes* and other early palaeoryctids, the latter may, however, be related to leptictids through such forms as *Kennalestes* and *Asioryctes* (Kielan-Jaworowska, 1969, 1975; McKenna, 1975 and pers. comm.).

Several European genera, *Diaphyodectes*, *Adapisoriculus*, and *Adunator* (medial and late Paleocene Cernay and Walbeck faunas), were recognized by Russell (1964) as leptictids. Guth (1962) described an exquisitely preserved leptictid skeleton from late Paleocene beds at Menat Basin, France, but made no formal assignment of the specimen. The aberrant *Pseudorynchocyon* from the early Oligocene Quercy Phosphorites was recently assigned by Sige (1974) to a new leptictid subfamily, the Pseudorynchocyoninae. Sige (1974) also allocated the medial Eocene *Leptictidium* to his newly established subfamily. A detailed consideration of the relationships of the alleged European leptictids to North American forms is presented elsewhere (Novacek, unpublished data).

Genus *Palaeictops* Matthew, 1899

Stypolophus Cope, 1880
Ictops: Cope, 1881
Parictops Granger, 1910
Diacodon: Matthew and Granger, 1918

Diagnosis.-- P^5 and upper molars not transverse nor anteroposteriorly compressed, with low bulbous cusps very narrow stylar shelves, small but distinct hypocones, very short anterior cingula, and conules situated labially at base of paracone and metacone. M^2 not significantly transversely wider than M^1. Parastylar spurs not strongly developed and ectoflexi not deep on M^2 and M^3. Paraconid on P_5 well developed. Molar trigonids not as elevated as in *Prodiacodon*. Skull (where known) with a single median sagittal crest and a very narrow zygomatic arch.

Type species.-- *Palaeictops bicuspis* (Cope, 1880) described as *Diacodon bicuspis* by Matthew and Granger (1918).

Geologic range.-- Wasatchian (early Eocene)-early Uintan (later Eocene).

Remarks.-- Species of *Palaeictops* can easily be distinguished from other known Paleocene and Eocene leptictids by their notable lack of such sectorial features as very transverse, anteroposteriorly compressed molars with sharp, elevated cusps, which indicate an emphasis on shearing and piercing in occlusion. The major difficulty arises in conveniently separating *Palaeictops* from the Oligocene leptictid *Leptictis* (Leidy, 1868). There are definite dental differences between the two genera but a series of species here referred to *Palaeictops* represent intermediate stages that grade easily into the condition represented in *Leptictis* (see below). The type species of *Palaeictops*, *P. bicuspis*, however, is clearly different from *Leptictis* in the presence of a single sagittal crest rather than double parasagittals, and in having nasal bones which are enlarged posteriorly. Van Valen (1967) expressed doubt as to whether parasagittal crests were universally present in *Leptictis* but this feature is in fact present without exception in the large sample (200 skulls) representing the genus. The double parasagittal crest therefore appears to be a useful diagnostic character in separating *Leptictis* from *Palaeictops*. Unfortunately, the single sagittal crest is clearly preserved only in *P. bicuspis*. Reference of other species to *Palaeictops* is based primarily on dental evidence, and consequently the assignment of species like *P. matthewi* is somewhat arbitrary. This is to be expected. *Palaeictops* is undoubtedly very closely related to *Leptictis* and one of its lineages probably gave rise to the latter.

Palaeictops bicuspis (Cope, 1880) Matthew, 1899

Fig. 3

Stypolophus bicuspis Cope, 1880, p. 746
Ictops bicuspis: Cope, 1881, p. 192; Cope, 1885, Pl. XXIXa, figs. 2 and 3
Palaeictops bicuspis Matthew, 1899
Diacodon bicuspis Matthew and Granger, 1918, p. 574-576, figs. 3-5

Diagnosis.-- P^4 with large, swollen paracone, very small anterior accessory cuspule, and small protocone. Stylar shelf on P^5 only present external to metacone. Hypocone present on P^5. Precingulum on P^5 and upper molars not extensive, terminating far short of lingual edge of protocone. P^4 lacking an anterior accessory cusp. P_4 heel is very small. P_5 with large bulbous paraconid, and minute cuspule at labial base of paraconid. Lower molars with bulbous rather than piercing cusps, trigonids not greatly elevated relative to talonids. M_3 with salient hypoconulid. Skull with single sagittal crest and nasals swollen posteriorly.

Type.-- AMNH 4802, skull and jaws

Type locality.-- Wind River Basin, Wyoming. Wind River Fm., Wasatchian (early Eocene).

Referred material.-- AMNH 4255, left mandible with broken M_1, M_{2-3} from Willwood Fm., Bighorn basin, Wyoming. Wasatchian.

Remarks.-- Cope (1880) originally described *Palaeictops bicuspis* as a species of *Stypolophus*, a taxon also containing several creodonts, and later (1881) transferred the species to the Oligocene genus *Ictops* (now considered a junior synonym of *Leptictis;* see Van Valen, 1967). The name *Palaeictops* was assigned by Matthew (1899) in a footnote of a biostratigraphic review. Matthew and Granger (1918) referred the species to *Diacodon,* but was later taken out of synonymy by Gazin (1952) who recognized the very reduced talonid of P_5 in *Diacodon alticuspis* as a character denoting its generic separation from *Palaeictops*.

The type of *Palaeictops* is a badly crushed skull, and the reconstruction of the specimen provided by Matthew and Granger (1918, Fig. 3 and 5, p. 575) takes some rather strong creative liberties. For example, the reconstruction shows the presence of three incisor alveoli in the upper jaw, while only two can actually be discerned on the specimen. The reconstruction of the skull shape is based primarily on the Oligocene *Leptictis* and its accuracy seems doubtful. However, at least the diagnostic cranial features of *P. bicuspis*, the single sagittal crest and the posteriorly flared nasal bones, are readily recognizable in the original specimen.

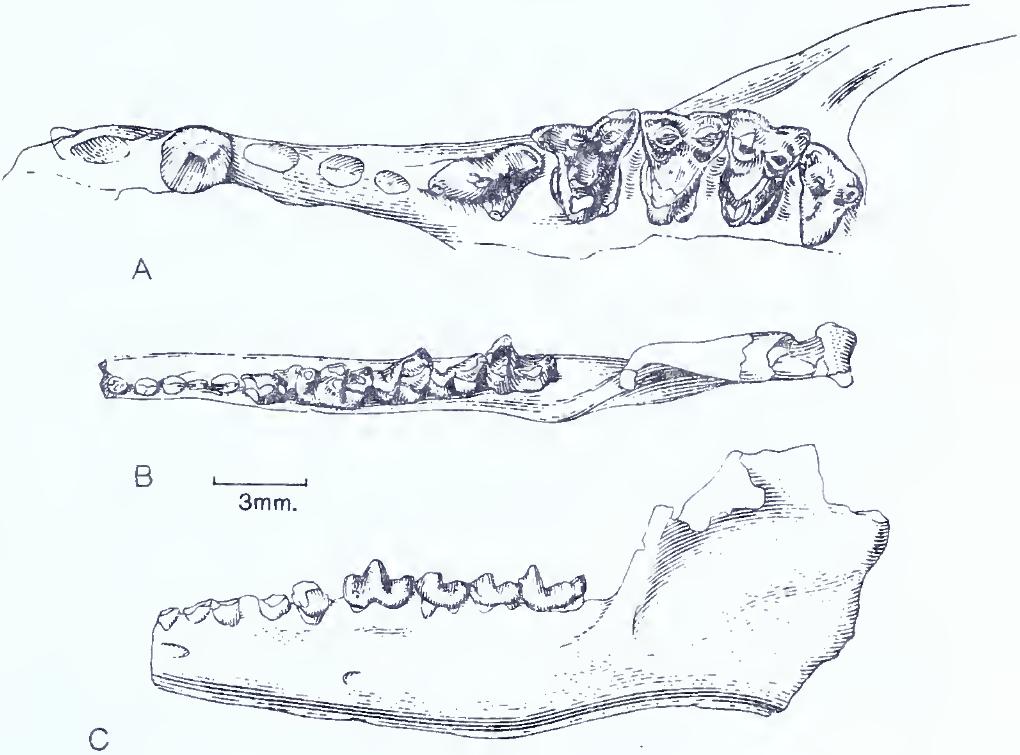

Fig. 3. *Palaeictops bicuspis* AMNH 4802 Type. A. Left maxilla with C, P^5, M^{1-3} and alveoli for I^3, (D) P^1, P^2, occlusal view. B. Left mandible with P_4 fragment, P_5, M_{1-3} and alveoli for (d) P_1, P_2, occlusal view. C. Same specimen as B, lateral view.

Palaeictops bridgeri (Simpson, 1959) Van Valen, 1967

Diacodon bridgeri Simpson, 1959; p. 1-5, fig. 1.

Diagnosis.-- Very similar to *Palaeictops bicuspis* in dental features but approximately 15% larger and $P_{\overline{5}}$ with a distinctly more open prefossid as a result of the anterolingual projection of the paraconid and the position of the metaconid more posterior to that of the protoconid. Talonid basins relatively broader than in *P. bicuspis*.

Type Specimen.-- AMNH 56032, a right lower jaw with $P_{\overline{5}}$-$M_{\overline{3}}$.

Type locality.-- Locality 6 of McGrew (1959) in the vicinity of Tabernacle Butte, Wyoming. Bridger Formation, Bridgerian (medial Eocene).

Remarks.-- In his original description of *Palaeictops bridgeri*, Simpson (1959) noted the strong similarity between this species and *P. bicuspis*. If not for its distinctive $P_{\overline{5}}$ characteristics *P. bridgeri* would be synonomous with the genotypic species. At the least, the two species appear to be very closely related. Simpson (1959) remarked that the trigonids in *Palaeictops bridgeri* are not particularly short or square; but this is not entirely accurate as the trigonids in this species have the relatively lower profile characteristic of *Palaeictops* in contrast to the higher, more piercing trigonid cusps of *Prodiacodon*.

Palaeictops bridgeri shows a close resemblance to the *Leptictis* species, *L. haydeni*, and *L. dakotensis* in lower cheek tooth morphology. However this Bridgerian species is distinguished from *Leptictis* in details characteristic of *Palaeictops*, namely a $P_{\overline{5}}$ paraconid set more lingually rather than central on the anteroposterior axis of the crown, less conical paraconids, and a more salient hypoconulid on $M_{\overline{3}}$.

Palaeictops multicuspis (Granger, 1910) Van Valen, 1967
Fig. 4

Parictops multicuspis Granger, 1910

Diagnosis.-- Large *Palaeictops* species with much deeper ramus than other species referred to the genus. Mental foramen below anterior root of $P_{\overline{2}}$. $P_{\overline{2}}$ trenchant with four cusps. $P_{\overline{4}}$ very large tooth; higher than $P_{\overline{5}}$, trenchant with very small, low anterior accessory cusps, two main cusps, and at least two low cusps on the shortened heel. All cusps aligned along the anteroposterior axis of the tooth. $P_{\overline{5}}$ with strong paraconid and minute cuspule at labial base of paraconid. $P_{\overline{5}}$ paraconid large, not well separated from metaconid, with prefossid interrupted labially by close approximation of paraconid with protoconid. Paraconid on molars set quite lingually and closely approximated to metaconid. $M_{\overline{3}}$ hypoconulid not so posteriorly projecting as in *Palaeictops bicuspis*.

Type Specimen.-- AMNH 14741, a left ramus with $P_{\overline{2}}P_{\overline{4}}P_{\overline{5}}M_{\overline{1-3}}$ and a right ramus with $P_{\overline{4}}P_{\overline{5}}M_{\overline{1-3}}$ and alveoli for double-rooted $P_{\overline{2}}$ and single rooted canine, and three incisors.

Type locality.-- Alkali Creek, (Buck Springs) of Wind River Basin, Wyoming. Lost Cabin beds, Wind River Formation, Wasatchian (early Eocene).

Remarks.-- The reference of this species to *Palaeictops* is provisional; it is primarily based on the low profile of the molar trigonids and the similarity of the $P_{\overline{5}}$ to that of *P. bicuspis* in the strong development of the paraconid and the presence of a minute cuspule at the labial base of the paraconid. Unfortunately, heavy wear on the molars renders an accurate estimate of trigonid elevation impossible. As is evident from the diagnosis of

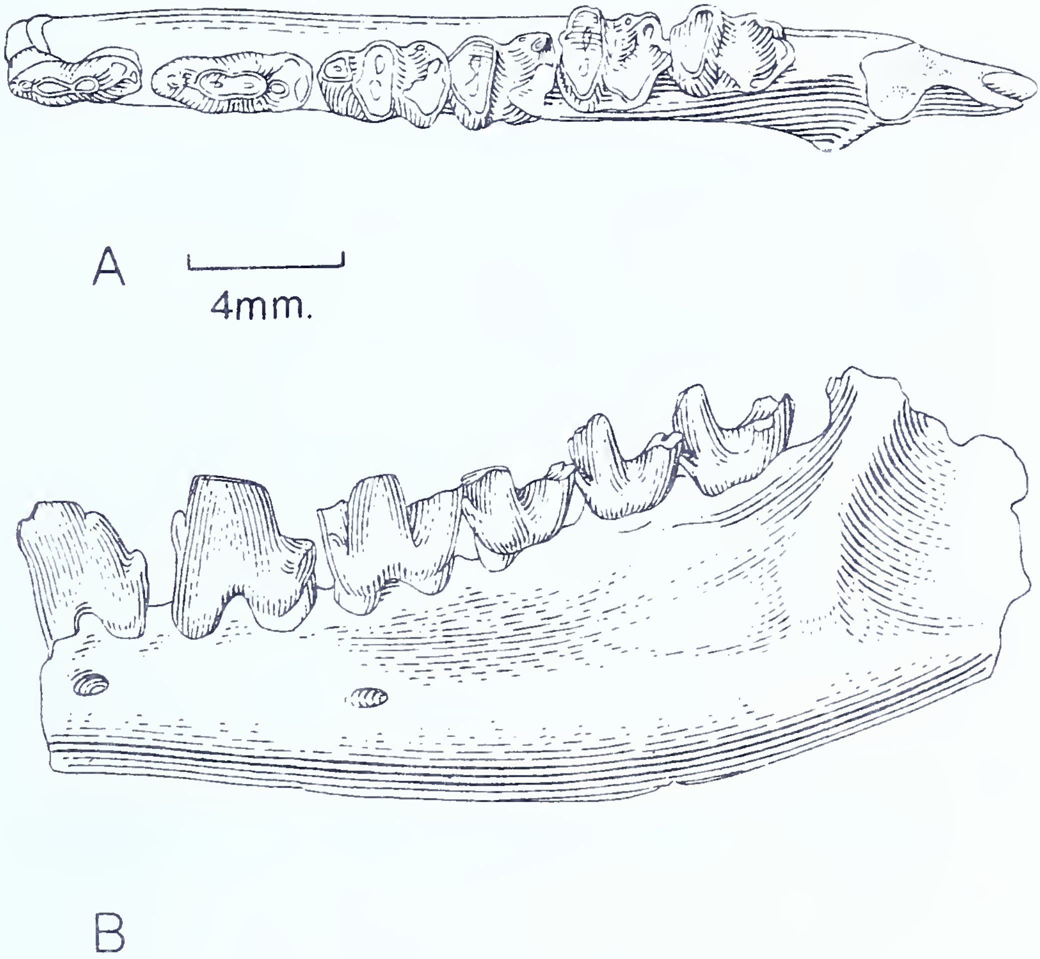

FIG. 4. *Palaeictops multicuspis.* AMNH 14741 Type. Left mandible with P_{4-5}, M_{1-3}, A. Occulusal view. B. Lateral view.

Palaeictops, upper molars are much more useful for purposes of identification than are lower molars.

The $P_{\overline{2}}$ and $P_{\overline{4}}$ of *Palaeictops multicuspis* are unique in their large size and in the development of several cusps. As in the dentitions of species of *Prodiacodon*, an anterior accessory cusp is present on $P_{\overline{4}}$ but the great size of this tooth relative to $P_{\overline{5}}$ differs from the condition observed in all *Prodiacodon* species.

I concur with Van Valen (1967, p. 235) that the characters of $P_{\overline{2}}$ and $P_{\overline{4}}$ (= Van Valen's $P_{\overline{3}}$) do not warrant recognition of *Palaeictops multicuspis* as a distinct genus.

Palaeictops matthewi new species
Figs. 5, 6

Diagnosis.-- Species of *Palaeictops* with lower dentition similar to *P. multicuspis* but 8% smaller and $P_{\overline{2}}$ simpler in morphology with only one main trenchant cusp and a basal posterior cuspule. $P_{\overline{4}}$ very large double-rooted tooth much higher than $P_{\overline{5}}$ with a minute anterior basal cuspule, a very large main cusp broadly connected with a slightly smaller, more posterior cusp, and a short transverse ridge on the posterior heel separated from the rest of the crown by a transverse trough. Trigonids in $P_{\overline{5}}$ and lower molars not greatly elevated relative to talonid. $P_{\overline{5}}$ metaconid set posterior to protoconid but not to the degree present in *P. bridgeri*. $P^{\underline{4}}$ high, enlarged tooth (relatively much higher than $P^{\underline{5}}$) with a very prominent paracone, smaller metacone, and low protocone. Apex of protocone set directly opposite the notch between the paracone and metacone. Very narrow cingula present anterior to paracone and posterior to metacone. $P^{\underline{5}}$ with very narrow stylar shelf continuous along labial border of crown and slight ectoflexus. Postcingulum well developed. Small parastyle and parastylar lobe, conules set labially at bases of paracone and metacone. Upper molars with labial conules. Precingula not elongate, terminating lingually nearly directly below the midpoint of the preprotocrista. $M^{\underline{1}}M^{\underline{2}}$ with distinct parastylar and metastylar spurs. Hypocones larger than in *Prodiacodon* but not so developed as in *Leptictis*. Tibia-fibula fused for most of their shaft lengths, as in *Leptictis*. Nasals swollen posteriorly (?) as in *Palaeictops bicuspis*.

Type specimen.-- P26904 (CMNH) lower mandible with C-$M_{\overline{3}}$, badly damaged skull with cheek teeth, partial skeleton including lumbar and caudal vertebrae, pelvis, femur, tibia, carpals, tarsals and phalanges.

Type locality.-- Cherard Park, Garfield Co., Colorado. Shire Member?, Wasatch Formation, Wasatchian (early Eocene).

Referred specimens.-- AMNH 17555. Skull fragments, partial lower jaws, and partial skeleton from Garcia Canon region, Colorado. Lower beds of Huerfano Formation, Wasatchian (early Eocene). P26481, fragmentary upper jaw with DP$^{\underline{4}}$, P$^{\underline{5}}$.

Etymology.-- Named after Dr. William D. Matthew, late 19th-early 20th century paleontologist who made significant contributions to the study of leptictids and many other Tertiary mammals.

Remarks.-- *Palaeictops matthewi* is an interesting species because it exhibits a dental morphology transitional between other species of *Palaeictops* and the Oligocene *Leptictis haydeni* and *L. dakotensis*. The similarity between the $P_{\overline{2}}P_{\overline{4}}$ morphology of the latter species and *P. matthewi* is striking. The only significant difference is the lack of an anterior accessory cusp in the $P_{\overline{4}}$ of *Leptictis*. The overall morphology of $P_{\overline{2}}P_{\overline{4}}$ is unique within the

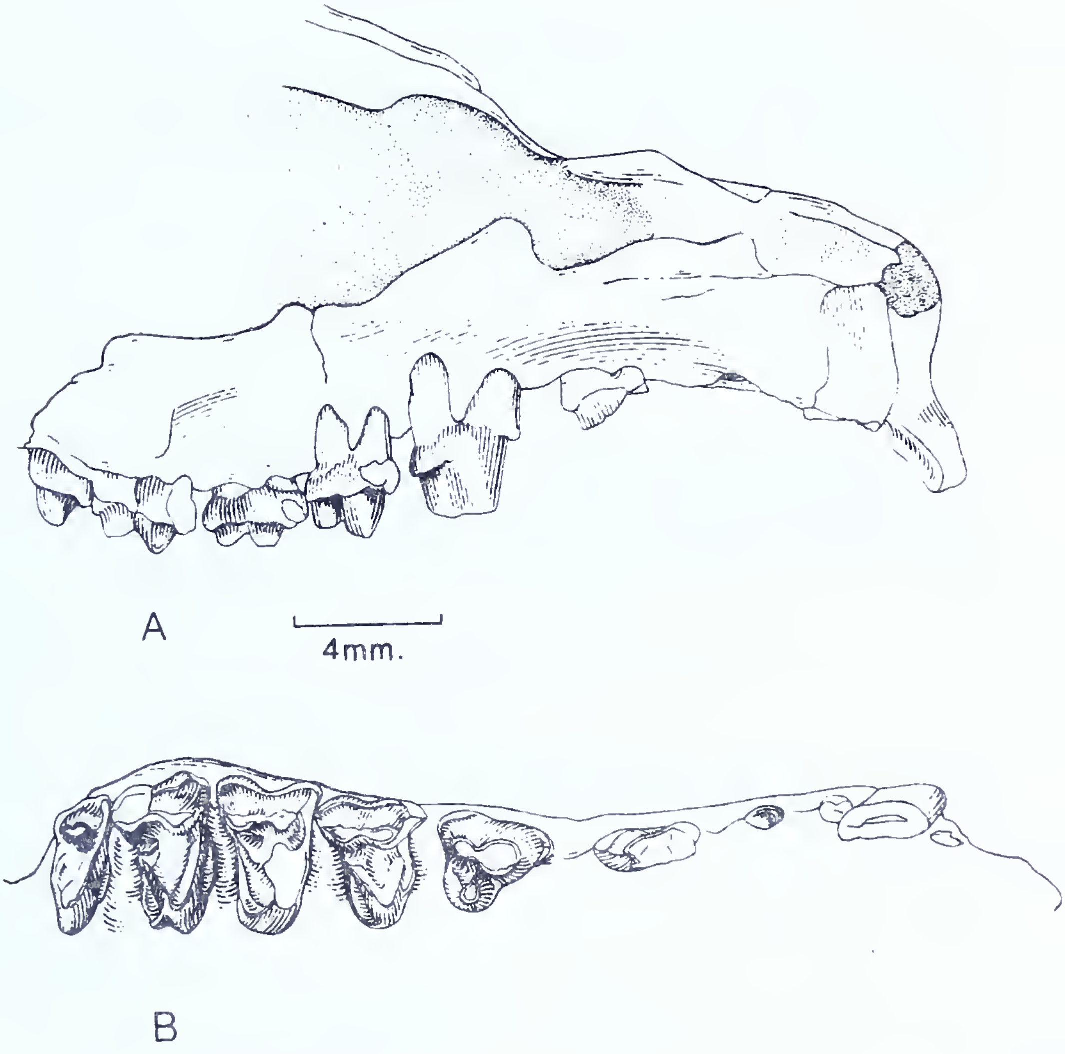

FIG. 5. *Palaeictops matthewi*. n.sp. CMNH 26904 Type. Fragmentary skull with canine root, P^2 fragment, P$^{4-5}$, M$^{1-3}$ and alveolus for (D)P^1. A. Laterial view. B. Occlusal view.

Leptictidae to *Leptictis* and *P. matthewi* and is here interpreted as a shared-derived character. Skeletal features in *P. matthewi* also strongly resemble those in *Leptictis*; particularly interesting is the common possession of tibia-fibula fusion for almost the total length of the shaft, a distinct departure from the more primitive condition represented in *Prodiacodon* where only the distal ends of the tibia-fibula are fused. There is, in fact, a strong enough resemblance of *P. matthewi* to *Leptictis* to make the generic assignment of this form somewhat arbitrary. However,

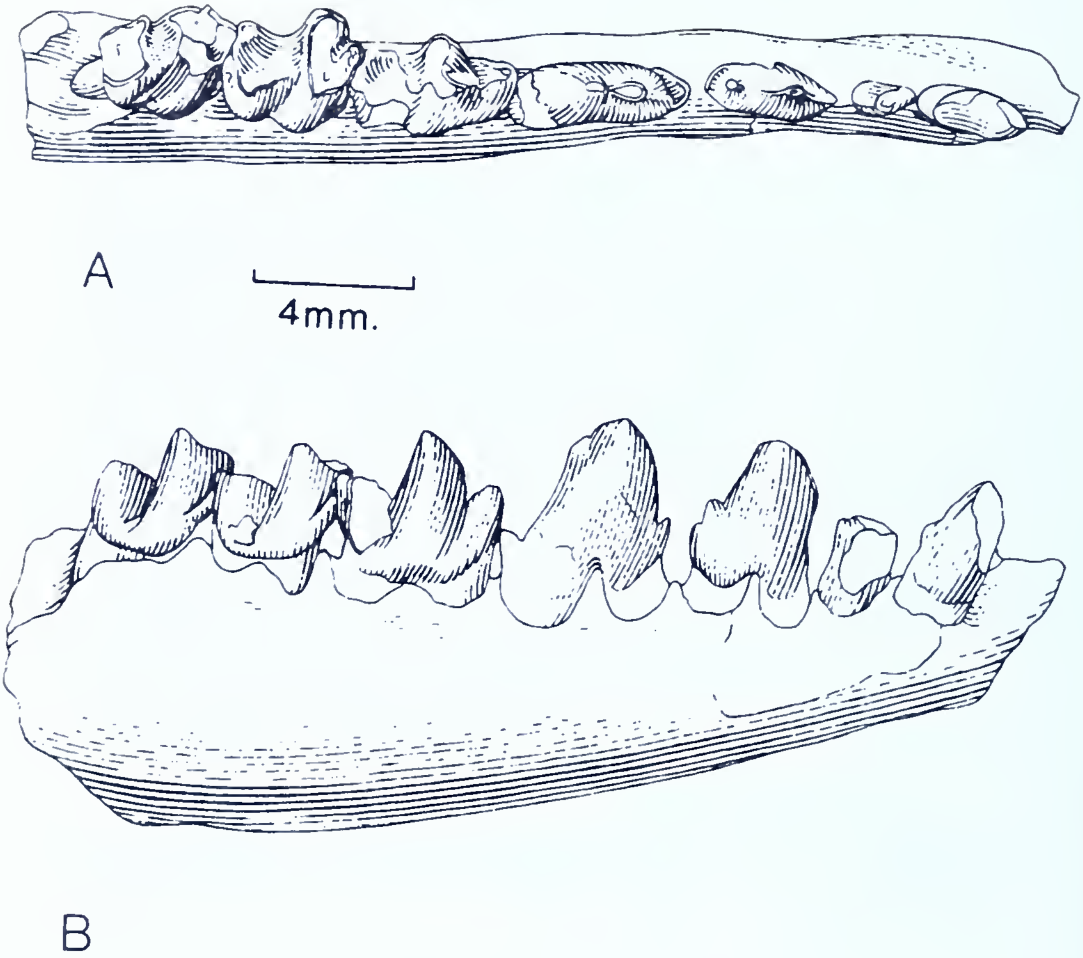

FIG. 6. *Palaeictops matthewi* n.sp. CMNH 26904 Type. Right mandible with (d)P_1,P_2, P_{4-5}, M_{1-2}. A. Occlusal view. B. Lateral view.

P. matthewi has not yet made the full transition in molar specializations: unlike *Leptictis* and like other species of *Palaeictops* the upper molars do not show the exaggerated swelling of the molar cusps, the strongly developed hypocones, the row of small cuspules on the posterior cingulum, and the lack of prominent parastylar and metastylar spurs on M^{1-2}. These differences are slight, to be sure, but would be expected when sampling forms that possibly represent intermediates between two major taxa. Unfortunately, the type skull of *P. matthewi* is too badly damaged to provide useful taxonomic information. It is not known, for instance, if *P. matthewi* had double parasagittal crests as in *Leptictis* or a single one as in *P. bicuspis*. The nasal bones appear to be enlarged posteriorly (as in *P. bicuspis* but not as in known skulls of *Leptictis*), however this observation may not be reliable due to damage in this region of the skull.

Palaeictops multicuspis resembles *P. matthewi* in having an enlarged $P_{\overline{4}}$ of very similar structure. However, the $P_{\overline{2}}$ in *P. multicuspis* is quite distinct in morphology, and this coupled with its significantly larger size seems sufficient evidence for keeping *P. multicuspis* specifically separate from *P. matthewi*.

Palaeictops sp.

A partial leptictid skull and jaws with dentition has been recovered from unit 24 (A beds) of the type section of the Tepee Trail Formation in the East Fork Basin, Fremont County, Wyoming (see Love, 1939; McKenna, 1972 for locality descriptions). This specimen and two other jaw fragments were kindly loaned to me for study by Dr. Malcolm McKenna, who is currently conducting field work and faunal analysis in the East Fork Basin. My interpretation that the specimens represent a new species of *Palaeictops* will be supported elsewhere with detailed descriptions, comparisons and illustrations.

Myrmecoboides Gidley, 1915

Myrmecoboides montanensis Gidley, 1915

Fig. 7

Diagnosis.-- Anterior premolars well spaced. $P_{\overline{1}}$ very small, single-rooted. $P_{\overline{4}}$ with paraconid and heel with basin and posterior cusp (D?)$P_{\overline{5}}$ paraconid considerably salient, prefossid open labially and lingually, heel elongate very narrow without hypoconulid. Molar trigonids not nearly as elevated as in *Prodiacodon*, paraconids situated very lingually, closely appressed to metaconid producing a "twinned" appearance. Molar paraconids and metaconids much higher than protoconids. $M_{\overline{3}}$ talonid elongate with salient hypoconulid. Entoconulid present on $P_{\overline{5}}$ and lower molars.

Type species.-- *Myrmecoboides montanensis*, middle Paleocene (Torrejonian) described by Gidley (1915) and later by Simpson (1937, p. 115-118, figs. 17-18).

Type specimen.-- USNM 8037. Left lower jaw with $P_{\overline{1}}$-$M_{\overline{3}}$.

Type locality.-- Gidley Quarry, Crazy Mountain Field, Sweetgrass County, Montana. Fort Union Formation, Torrejonian (middle Paleocene).

Referred material.-- USNM 9552, $P^{\underline{5}}$-$M^{\underline{3}}$ (see discussion below).

Remarks.-- In the original description of *Myrmecoboides*, Gidley (1915) allocated this genus to the Marsupialia, noting its strong similarities with *Myrmecobius*. Simpson's (1937) re-analysis

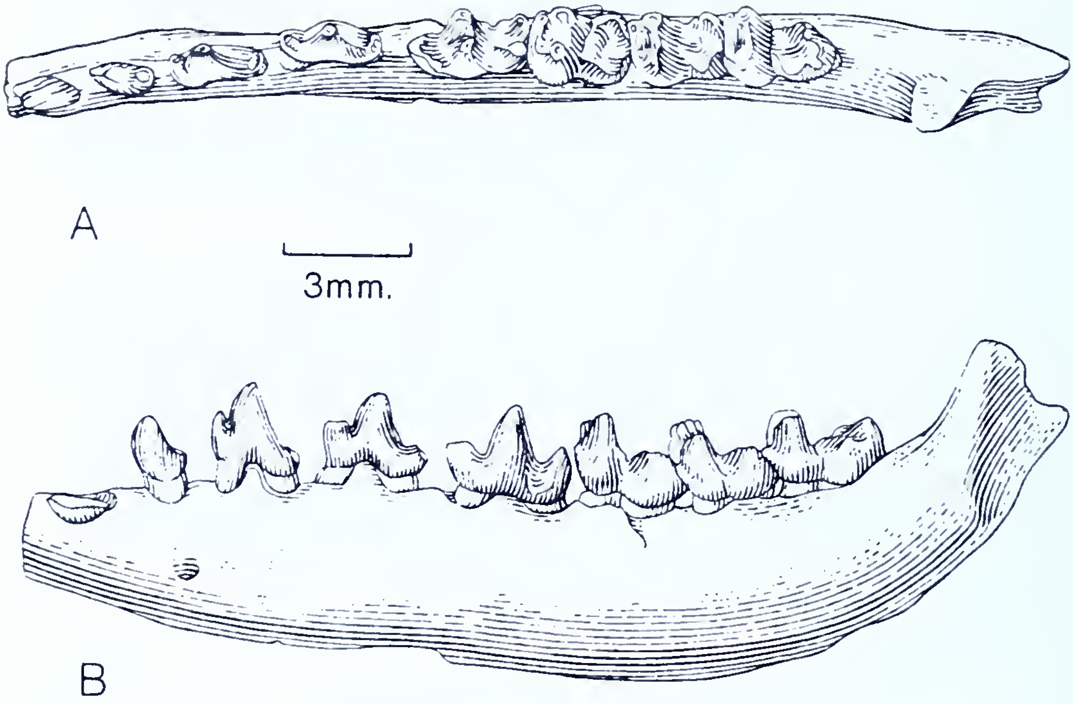

FIG. 7. *Myrmecoboides montanensis* USNM 8037 Type. Left Mandible with (D)P_1, P_2, P_{4-5}, M_{1-3}. A. Occlusal view. B. Lateral view.

demonstrated that *Myrmecoboides* is best referred to the Leptitidae, but as he noted, its position in the family is isolated. Particularly striking is the unique structure of the molar trigonids, namely, the lingual position of the paraconid and its close appression to the metaconid and the much higher relief of the "twinned" metaconid and paraconid relative to the protoconid.

An upper dentition (P^5-M^3, USNM 9552) from Gidley Quarry referred by Simpson (1937) to *Myrmecoboides montanensis* shows a strong resemblance to corresponding teeth in *Prodiacodon puercensis*, thus suggesting a relationship with the latter. I suspected (in agreement with the unpublished opinions of Craig Wood) the reference of this upper set of cheek teeth to *M. montanensis* was erroneous. Percy Butler (personal communication) has however carefully analyzed the occlusal relationships of the upper and lower dentition and convinced me that the association is probably valid. I am still open to the possibility that USNM 9552 might represent the upper cheek teeth of *Prodiacodon furor*, a new species from Gidley Quarry (see below).

Prodiacodon Matthew, 1929

Diacodon: Matthew and Granger, 1918; Gazin, 1952
Palaeictops: Van Valen, 1967

Diagnosis.-- P^5 and molars transverse, anteroposteriorly compressed with sharp piercing cusps. P^5 hypocone vestigial or absent. Conules set lingually, not at the base of paracone and metacone as in *Palaeictops* and *Leptictis*. Precingula on P^5 and molars long, nearly reaching anterolingual corner of the crown. Hypocone on upper molars very short relative to protocone. Paraconule lingual to metaconule on M^1-M^2. Paraconule "doubled" where upper molars are known. Parastylar lobes on M^1 and M^2 prominent and ectoflexi deep. Lower molars with sharp cusps. Trigonids high and anteroposteriorly compressed. Paraconid not closely "twinned" with metaconid and not higher than protoconid as in *Myrmecoboides*.

Type species.-- *Prodiacodon puercensis*.

Remarks.--*Prodiacodon* is a broadly defined genus which includes forms emphasizing a sectorial mode of occlusion. The molar cusps are high and piercing. Except for the development of the hypocones and the lingual cingula, the complexity of the P^4 and the molariform structure of P^5, *Prodiacodon* resembles other early eutherians in the general structure of the molar morphology, and it is quite plausible that the molar structure in *Prodiacodon* is more primitive than that seen in *Palaeictops* and *Leptictis*.

It follows that the concept of *Prodiacodon* presented here is based primarily on dental characters which are primitive for the Leptictidae. However, all species of *Prodiacodon* can be separated from their most closely related plesiomorphic sister taxon, *Gypsonictops*, in the common possession of characters derived relative to the latter—narrow stylar shelves, hypocones invariably present on the upper molars, paraconids always present on P_5, and only 4 premolars.

Prodiacodon has been traditionally recognized as a monotypic genus, but here includes various species formerly allocated to both *Diacodon* and *Palaeictops* (see Van Valen, 1967).

Prodiacodon puercensis (Matthew and Granger, 1918) Matthew, 1929

Fig. 8

Diacodon (Palaeolestes) puercensis Matthew and Granger, 1918, p. 576, 579, figs. 6-9.

Diagnosis.-- P^4 paracone not greatly swollen anteriorly. P^4 protocone subequal with metacone in height; anterior and posterior accessory cuspules present. P^5 with paracone and metacone broadly joined, and hypocone vestigial or absent but pre- and postcingula present. Molars with very small hypocones and elongate precingula. "Doubled" paraconules present on M^2. P_4 with small anterior accessory cusp, large bulbous medial cusp, small posterior cusp, and a short heel with a small cuspule. P_5 paraconid very small; talonid with 4 cusps. Entoconulids present on lower molars. M_3 talonid with 5 cusps. Skeleton differs from that in *Leptictis* in 1) tibia-fibula fused only at the distal ends, shafts being wholly free, 2) distal parts of astragalus and calcaneum considerably shorter, and 3) first digit longer.

Type specimen.-- AMNH 16011, maxillary fragment with P^5, edentulous lower jaw fragments, humerus, femur, tibia, fibula, tarsals, carpals, and phalanges.

Type locality.-- Torrejon Arroyo, San Juan Basin, New Mexico. Nacimiento Formation, Torrejonian (middle Paleocene).

Referred material.-- AMNH 16748, maxillary with P^2-M^3, mandible with P_4-M_3; partial skeleton. AMNH $_5$16598 mandible with P_5-M_3 and associated maxillary with partial P^5, M^{1-3}, Torrejon Arroyo. AMNH 703, left femur, astragalus. Rio Torrejon, San Juan Basin, Nacimiento Formation.

Remarks.-- *Prodiacodon puercensis* was originally recognized as a subgenus of *Diacodon* by Matthew and Granger (1918) who assigned the (subgeneric) name *Palaeolestes*. Matthew (1929) later raised this form to generic rank and named it *Prodiacodon*, as the name *Palaeolestes* was preoccupied.

The overall similarities of the skeleton of *Prodiacodon* to that of *Leptictis* were noted by Matthew and Granger (1918). These authors viewed *Prodiacodon puercensis* as "...an ancestral type of the leptictine phylum", but details of dental morphology, such as the 5-cusped talonid in M_3, the multi-cusped P_4, and the "doubled" paraconule in M^{1-3}, preclude an argument for its direct ancestry to *Palaeictops* or other species of *Prodiacodon*. *P. puercensis* is best viewed as early offshoot of the *Prodiacodon* group. It is interesting to note that the above cited "primitive" features in the skeleton of *P. puercensis* correspond with the hypothesis based on dental evidence that *Prodiacodon* is a primitive leptictid genus.

Prodiacodon tauricinerei (Jepsen, 1930b)

Diacodon tauricinerei Jepsen, 1930b, p. 124-126, pl. III, fig. 1-4.
Palaeictops tauricinerei Van Valen, 1967
Diacodon pineyensis Gazin, 1952
Palaeictops pineyensis Van Valen, 1967

Diagnosis.-- Similar to *Prodiacodon puercensis* but smaller with more transverse and anteroposteriorly compressed molars. Hypocone present on P^5. P^5 stylar shelf very narrow but present external to metacone. Paracone and metacone on P^5 not broadly joined. Like *P. puercensis* "doubled" paraconule present on M^2.

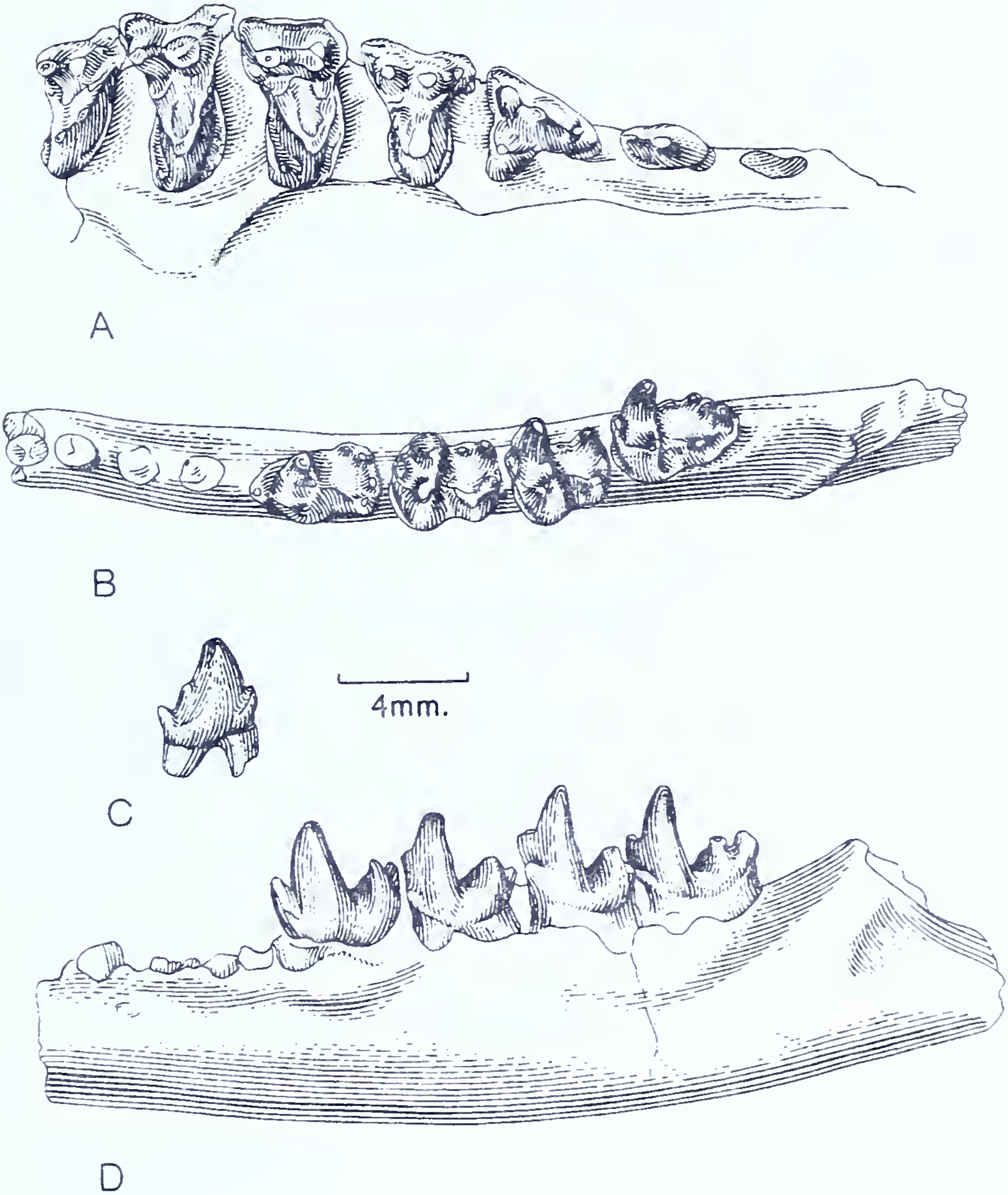

FIG. 8 *Prodiacodon puercensis* AMNH 16748. A. Right maxillary fragment with P^2, P^{4-5}, M^{1-3} and alveolus for (D)P^1, occlusal view. B. Left mandible with P_5, M_{1-3} and alveoli for P_2, P_4, occlusal view. C. Right P_4, lateral view. D. Same specimen as C, lateral view.

(d) P_1 and P_2 closely situated and procumbent. P_4 with five cusps, second cusp from anterior largest; heel longer than *P. puercensis*. Anteriormost cusp on P_4 small, but larger than in *P. puercensis*. P_5 paraconid larger than in *P. puercensis*, well separated from protoconid and metaconid, prefossid open both labially and lingually. P_5 talonid with 4 cusps. Metaconids higher than protoconids on M_{1-2}.

Type specimen.--PU 13104, right and left? lower jaw with C-M_3. Maxillary with I^2-M^3, crushed skull.

Type locality.-- "Shale Pocket" one and one-half miles south of Dorsey Creek, and two miles south of Otto-Basin road, Bighorn Basin, Bighorn County, Wyoming. Gray Bull beds, Willwood Formation, Wasatchian (early Eocene).

Referred specimens.-- PU 13267, lower jaw, incisors preserved on right side. Locality same as type (Jepsen, 1930b). PU 14726, maxillary with right and left C-M^3. AMNH 80023, right mandible fragment with P_5-M_3, East Alheit Pocket, Four Mile Creek, Moffit County, Colorado. Wasatch Formation. AMNH 80695, left mandible fragments with partial P_4, P_5, M_2, M_3. S. Elk Creek, Bighorn Basin, Wyoming. Wasatchian. AMNH 48763, right mandible P_5, M_3. 88 Quarry, Arroyo Blanco, New Mexico. San Jose Formation, Wasatchian. AMNH 12831, left mandible with P_5-M_3 right maxillary fragments with right P^5, M^2; left maxillary fragments with M^{1-3}. Bridger Creek, Wind River Basin, Wyoming. Wind River Formation, Wasatchian (See Matthew and Granger, 1918, p. 572-573). USNM 19204, left mandible with fragments of P_5, M_{1-3}. Big Piney, Sublette County, Wyoming. Knight Member, Wasatch Formation, Wasatchian. Described as the type of *Diaeodon pineyensis* by Gazin, 1952. Five isolated teeth from Powder River local fauna. Wasatchian (Delson, 1971, p. 324-325).

Remarks.-- *Prodiacodon tauricinerei* was first described by Jepsen (1930b) who noted that "Compared with other Diacodons, this species has molars with unusually small anteroposterior diameters and great linguo-labial dimensions". This character is more exaggerated than in *P. puercensis* but the dental differences between the two forms are less than generic. *P. tauricinerei* differs from *P. puercensis* in having smaller, more transverse molars, a greater number of cusps and a longer heel on P_4, and other characters noted in the above diagnosis.

It appears that many variously named early Eocene leptictids are referable to *Prodiacodon tauricinerei*. These include an upper and lower jaw in association from the Wind River Basin (AMNH 12831) referred by Matthew and Granger (1918) to *Diacodon alticuspis* and *Diacodon pineyensis* (Gazin, 1952). The latter was represented only by a fragmentary P_5 and M_{1-3} but these teeth are nearly identical to corresponding teeth in the type of *P. tauricinerei*, although they are slightly larger with a more anteroposteriorly compressed trigonid on M_2. Such differences are ascribed here to intraspecific variation.

Prodiacodon concordiarcensis Simpson, 1935, p. 228

Fig. 9, 10

Diacodon concordiarcensis (Gazin, 1956) Van Valen, 1967.
Diacodon pearcei Gazin, 1956

Diagnosis.-- Much smaller than *Prodiacodon puercensis* and *P. tauricinerei*. $dP_{\bar{1}}P_{\bar{2}}P_{\bar{4}}$ trenchant "mitten shaped" in lateral view. $P_{\bar{2}}$ and $P_{\bar{4}}$ with minute anterior accessory cuspule, large middle cusp, and small, very low posterior cusp. $P_{\bar{4}}$ much lower than $P_{\bar{5}}$. $P_{\bar{4}}$ heel separated anteriorly from main cusp by a continuous transverse trench. $P_{\bar{5}}$ talonid anteroposteriorly shorter than *P. puercensis* and *P. tauricinerei*. $P_{\bar{5}}$ and molars with three (not four) cusps on talonids. $M_{\bar{3}}$ trigonid with paraconid more nearly central in position than in *P. puercensis* and *P. tauricinerei*.

Type.-- USNM 9637, left mandible fragment with $P_{\bar{2}}$, $P_{\bar{5}}$, and $M_{\bar{3}}$.

Type locality.-- Gidley Quarry, Crazy Mountain Field, Sweetgrass County, Montana. Fort Union Formation (Lebo Member). Torrejonian (middle Paleocene).

Referred specimens.-- AMNH 35693, right mandible with $P_{\overline{1,2,4}}$, $M_{\overline{1-3}}$, from type locality. AMNH 35694, right lower jaw with $P_{\overline{2,4}}$ from type locality. USNM 20970, left mandible fragment with $P_{\bar{2}}$-$M_{\bar{1}}$ from Saddle Locality, Bison Basin at South Rim County, Wyoming. Fort Union Formation. Tiffanian (later Paleocene). Described as the type of *Diacodon pearcei* by Gazin, 1956.

Remarks.-- *Prodiacodon concordiarcensis* is the smallest known leptictid and is easily distinguishable from other species of *Prodiacodon* by this character. The curious "mitten-shaped" morphology of $P_{\overline{1,2,4}}$ and the reduced size of $P_{\bar{2}}$ relative to $P_{\bar{4}}$ in this species are also unique specializations for the family and a close affinity with later members of *Prodiacodon* seems unlikely.

In his discussion of "*Diacodon pearcei*" Gazin commented (1956, p. 17) on "the closeness of resemblance between *D. (Diacodon) concordiarcensis* and *D. (Diacodon) pearcei*". The similarity between the two species is indeed too great to keep them specifically separate and *D. pearcei* is here made a junior synonym of *P. concordiarcensis*. Thus evidence is provided for a leptictid lineage that probably underwent major reduction in size by Torrejonian times, a trend seen to occur in some later leptictid lineages as well.

Prodiacodon furor new species

Fig. 11

Diagnosis.-- Similar to *Prodiacodon concordiarcensis* but 28% larger with $P_{\bar{2}}$ and $P_{\bar{4}}$ of simpler construction, consisting only

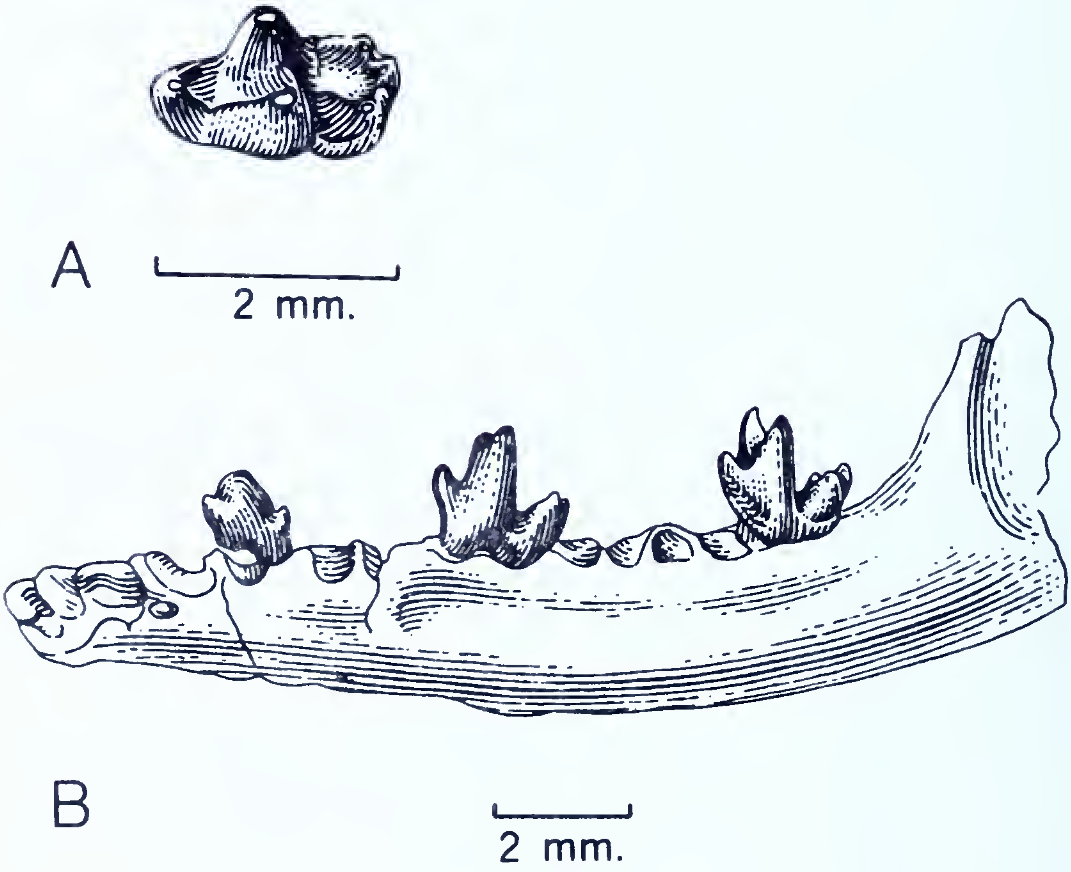

FIG. 9. *Prodiacodon concordiarcensis* USNM 9637 Type. A. Left P_5, occlusal view. B. Left mandible with P_2, P_5, M_3, lateral view.

of a high recurved cusp and a minute basal posterior heel. $P_{\bar{2}}$ subequal to $P_{\bar{4}}$ in height. $P_{\bar{4}}$ slightly lower than $P_{\bar{5}}$. Paraconid in $P_{\bar{5}}$ blade-like, directly anterior to protoconid. Talonid of $P_{\bar{5}}$ and molars short anteroposteriorly as in *P. concordiarcensis* but not in *P. puercensis* or *P. tauricinerci*. $P_{\bar{5}}$ metaconid of much larger basal dimensions and situated more posteriorly than protoconid. Metaconid on lower molars much higher and more swollen than protoconid. Four cusps are present on molar talonids as in *P. puercensis* and *P. tauricinerei*.

Type specimen.-- AMNH 35291, partial right mandible with $P_{\bar{2}}$, $P_{\bar{4}}$, $P_{\bar{5}}$.

Type locality.-- Gidley Quarry, Crazy Mountain Field, Sweetgrass County, Montana. Lebo Unit of Fort Union Formation, Torrejonian (middle Paleocene).

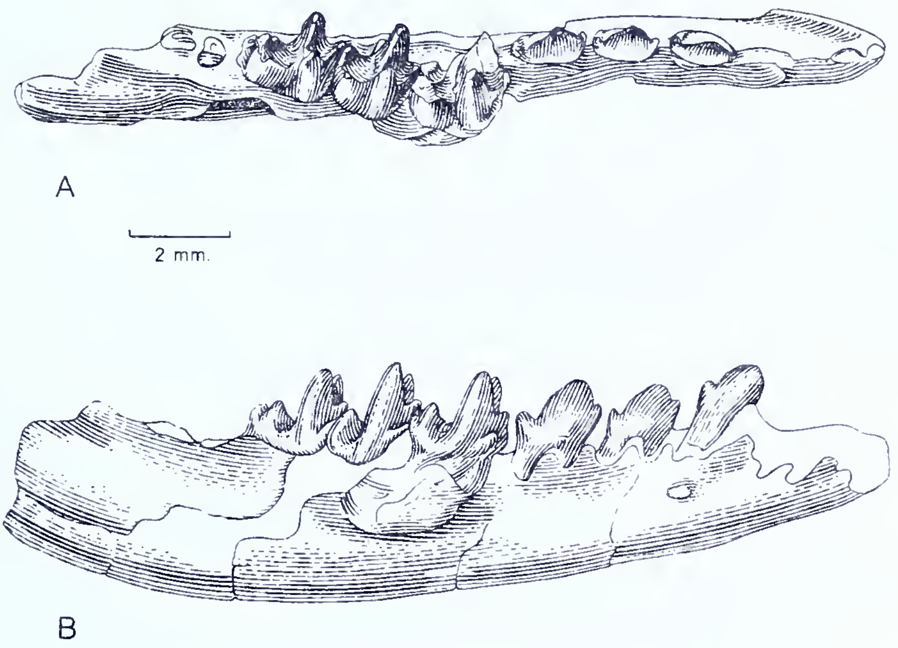

FIG. 10. *Prodiacodon concordiarcensis* AMNH 35693, right mandible with P_2, P_4,M_{1-3}. A. occlusal view. B. Lateral view.

Referred specimens.-- AMNH 35290, partial right mandible with $M_{\overline{1-2}}$. AMNH 35289, partial left mandible with $P_{\overline{5}}$, $M_{\overline{1-2}}$. Both from type locality.

Etymology.-- *furor* L. craziness. Refers to general region where specimens were collected. All known specimens are from Gidley Quarry in Crazy Mountain Field, Montana.

Remarks.-- With the recognition of *Prodiacodon furor*, Gidley Quarry shows a diversity of leptictids. At least two other species, *Myrmecoboides montanensis* and *P. concordiarcensis*, are also represented at this locality. It is quite possible that the upper dentition from Gidley Quarry referred by Simpson (1937) to *M. montanensis* might belong to *P. furor*, as the upper teeth are of proper size and shape for occlusion with the lowers. This would explain the strong resemblance of this specimen to upper molars of *P. puercensis*.

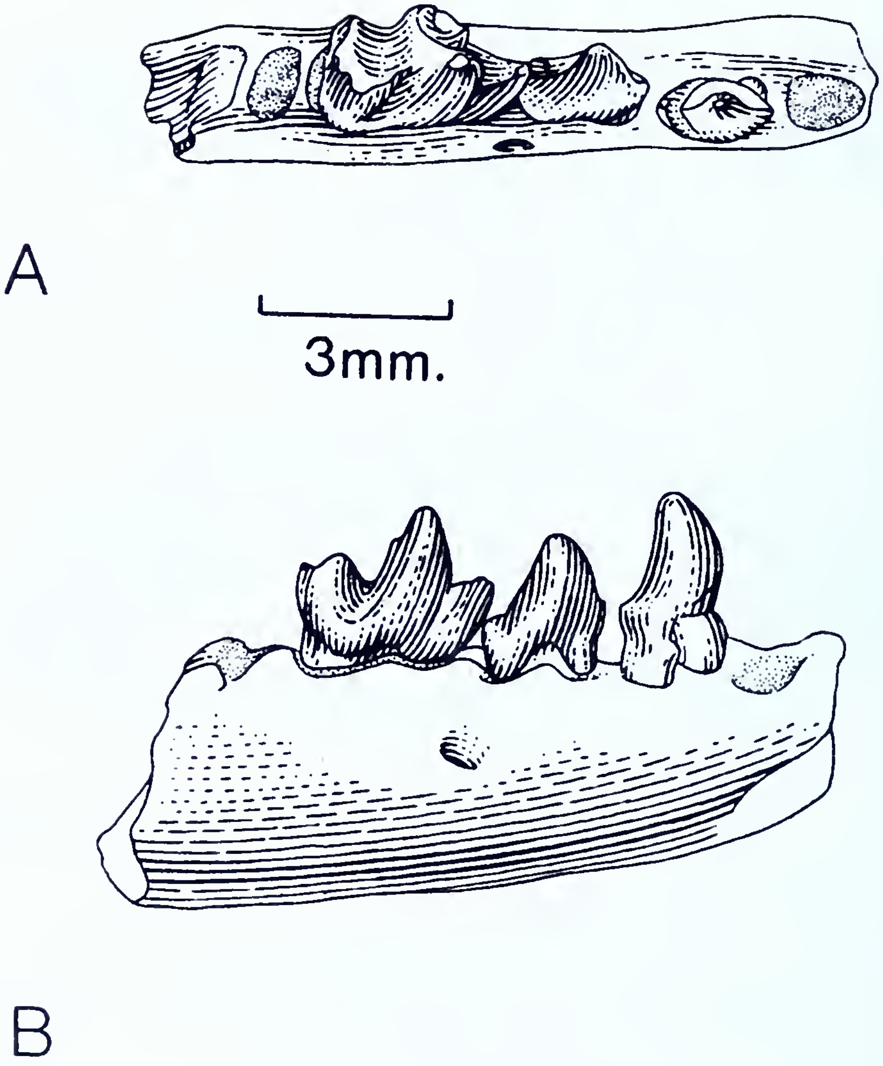

FIG. 11. *Prodiacodon furor* n. sp. AMNH 35291 Type, right mandible fragment with P_2, P_{4-5}, and alveolus for (D)P_1. A. Occlusal view B. Lateral view.

P. furor shows a strong similarity to *P. tauricinerei*, suggesting a possible close relationship with this younger early Eocene species. However, the enlarged and posteriorly situated $P_{\overline{4}}$ metaconid, in *P. furor* a character here considered as derived on the basis of its uniqueness within the Leptictidae, precludes any direct ancestor-descendant relationship between the two species.

Prodiacodon crustulum new species

Figs. 12, 13

Diagnosis.-- Upper molars similar to those in *Prodiacodon puercensis* but smaller with wider stylar shelves, smaller hypocones, shorter and smaller (in basal dimensions) metacones relative to paracones. A small cusp (stylocone) is present in some specimens on the labial edge of the crown at the junction with the preparacrista. Conules well developed and situated on the pre- and postprotocrista closer to the apex of the protocone than to the paracone and metacone bases. Paraconule higher than the metaconule. As in *Prodiacodon puercensis*, a small cuspule is present adjacent and anterolabial to the paraconule. Precingulum "crenulated" with series of folds. P^2 with pre- and postcingula. M_1 and M_2 talonids differ from those in *P. puercensis* in having only three cusps, lacking an entoconulid. Entoconulid present on M_3.

Type specimen.-- UCMP 114990, left M^1 .

Type locality.-- V-74122, Biscuit Springs locality, Garfield County, Montana, Tullock Formation, Puercan (early Paleocene).

Referred material.-- LACM 32970, right M^1 from V-72134, Garbani locality #9, Tullock Formation, Garfield County, Montana. UCMP 114993, left broken P_5, UCMP 114991-2, lower molars from V-74123 Yellow San Hill #1, Tullock Formation. UCMP 114971, 114973, 114975, 114976, 114977, 114980, 114988, upper molars. UCMP 114972, left P^5. UCMP 114974, 114979, left ?P^4's. UCMP 114978, right P_5 fragment. UCMP 114981, 114986, M_1's or M_2's. UCMP 114985, left M_3 from V-74122 - type locality. All localitites from Tullock Formation, Puercan, (early Paleocene).

Etymology.-- *crustulum* L. biscuit. Refers to the type locality, Biscuit Springs.

Remarks.-- Although only isolated teeth can be referred to this new Puercan species, enough characters are present to indicate its possible affinities and provide some insight on the relationship of very early leptictids. Most interesting is its close resemblance in some features of the upper molars to *Gypsonictops hypoconus* (Simpson, 1927). In both species a small cusp (?stylocone) is present posterior to the parastyle and labial to the paracone, the stylar shelf is moderately wider than those in *Palaeictops* or other species of *Prodiacodon*, and the hypocone is a very low cusp. Unlike *G. hypoconus* and like *Prodiacodon puercensis*, the precingulum has a slight rise or crest, the conules are more lingual in position, and the paraconule is "doubled", the main cusp being bordered anterolingually by a smaller cusp. In fact, *P. crustulum* shows a strong overall dental similarity to *P. puercensis* while representing a stage of dental development intermediate between that observed in *Gypsonictops hypoconus* and that

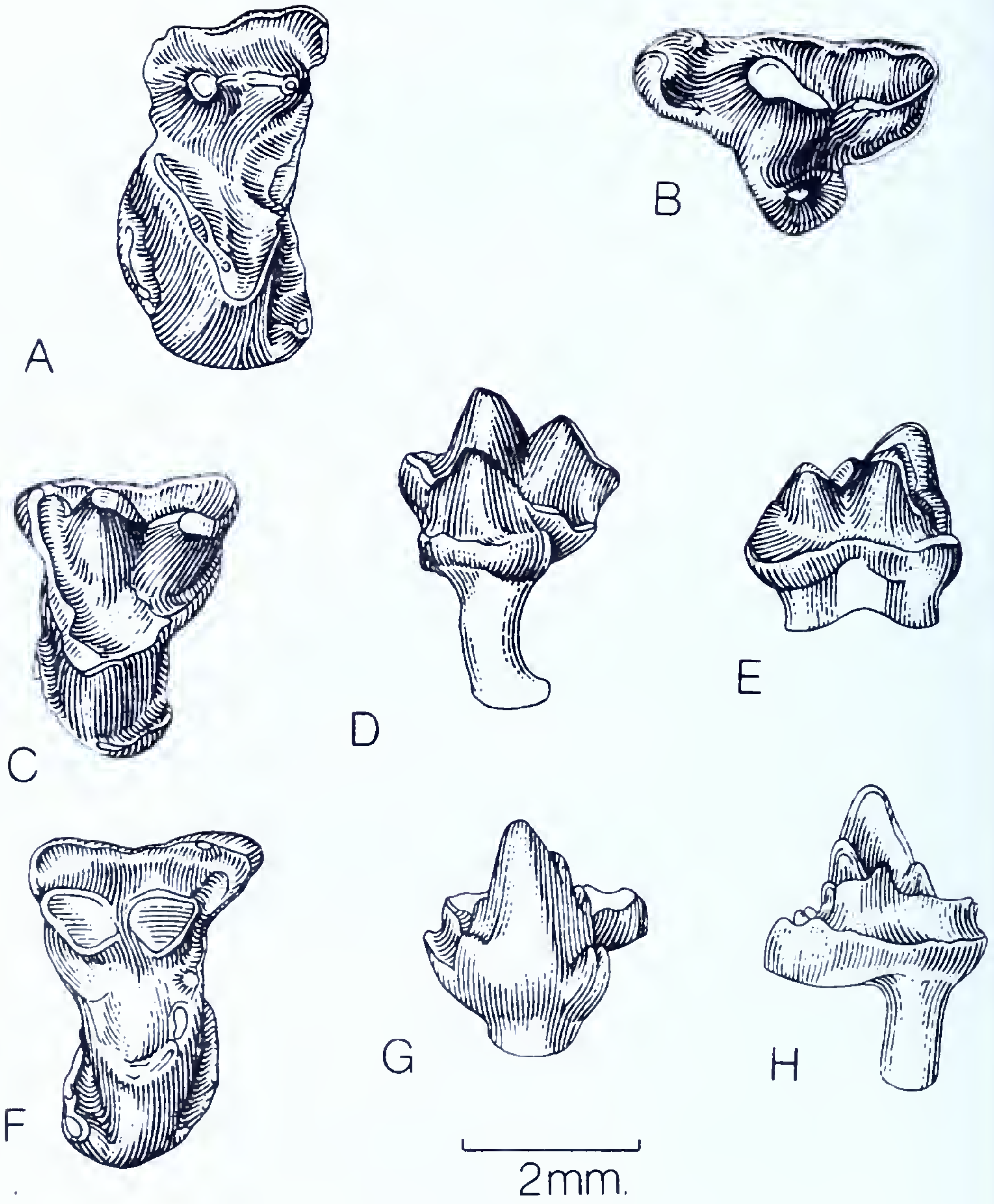

FIG. 12. *Prodiacodon crustulum* n. sp. A. UCMP 114990 Type, M^1, occlusal view. B. UCMP 114979, left P^4, occlusal view. C. UCMP 114972, left P^5 ? occlusal view. D. Same, lingual view. E. Same, labial view. F. UCMP 32970, right M^1, occlusal view. G. Same, lingual view. H. Same, labial view.

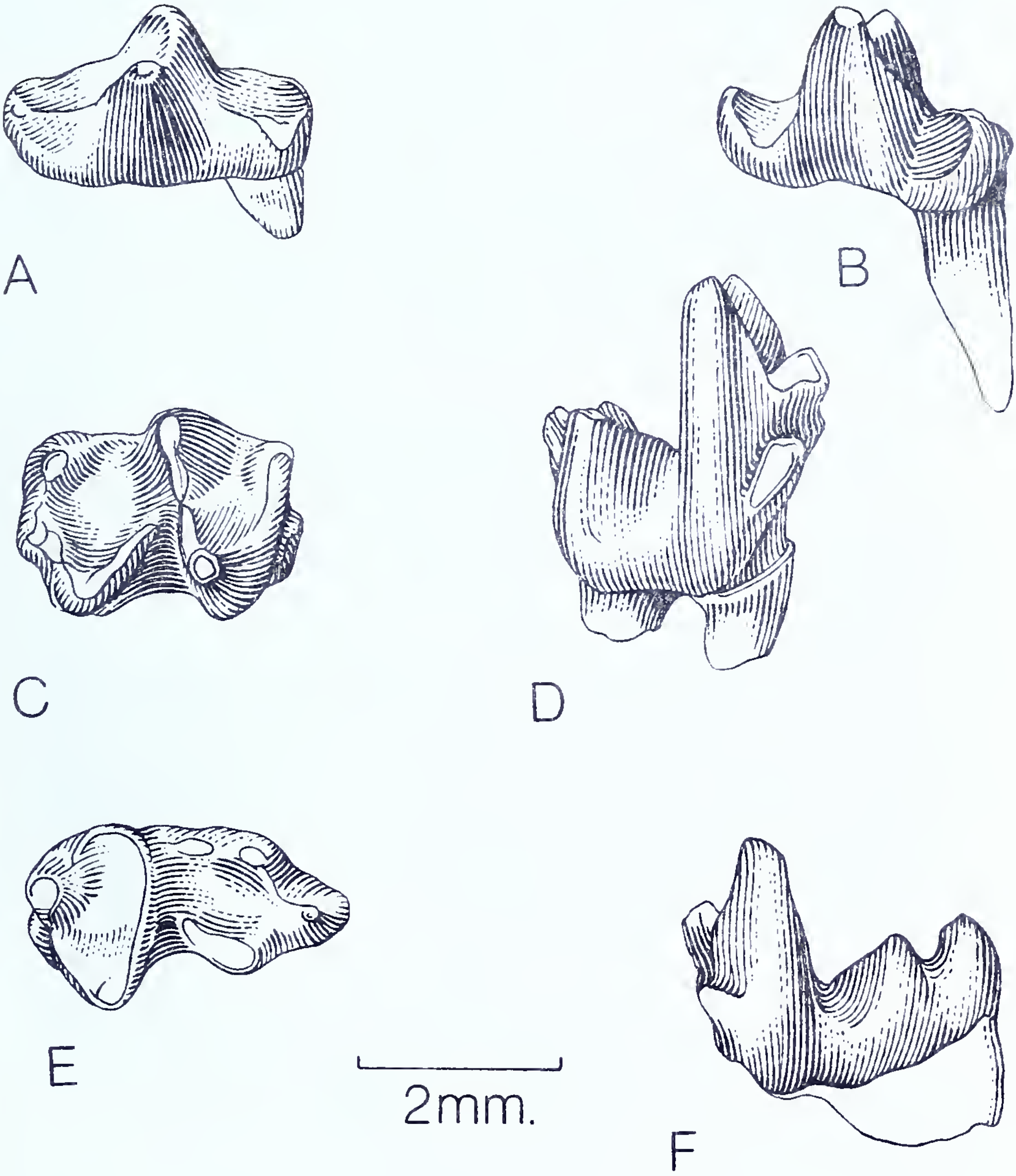

FIG. 13. *Prodiacodon crustulum* n.sp. A. UCMP 114982, left P_5?, occlusal view. B. Same labial view. C. UCMP 114986, right M_2, occlusal view. D. Same, labial view. E. UCMP 114985, left M_3, occlusal view. F. Same, labial view.

in *Prodiacodon*. Accordingly, *P. crustulum* is regarded here as the most primitive known Tertiary leptictid.

Leptictidae?

A few named leptictids are not recognized in this study because the referred material is too poor to allow any definite assignment. Russell (1929, p. 173-175) named a species *Diacodon septentrionalis* from the late Paleocene Cochrane 1 locality of Alberta. The referred material consists of an $M_{\overline{3}}$ and an $M_{\overline{1}}$ or $M_{\overline{2}}$. The high relief of the trigonid cusps suggests a reference to *Prodiacodon* rather than *Palaeictops*, but on the basis of the meager material it is impossible to determine whether these molars are assignable to a new species, *P. puercensis, P. tauricinerei, D. alticuspis,* or a pantolestid.

Gazin (1949) described a new genus and species, *Hypictops syntaphus,* from Bridgerian of western Wyoming based on a right upper cheek tooth dentition (USNM 13445). The outline and dimension of the teeth are so strikingly similar to those of *Leptictis dakotensis* as to suggest conspecificity, but the molars themselves are so badly worn that few, if any, important details are preserved. Even if well preserved, it is highly doubtful that this specimen would serve as evidence for a distinct genus.

Stock (1935) referred a fragmentary lower jaw with an $M_{\overline{3}}$ (CIT 16791) from a Brea Canyon locality (CIT locality 150) Sespe Formation, "late" Eocene, southern California, to the Leptictidae, but unfortunately this specimen cannot be relocated in the present CIT collections (recently acquired by LACM). The identification of this specimen as a leptictid jaw is questioned because the published description and illustration of the $M_{\overline{3}}$ does not eliminate the specimen from possible reference to palaeoryctids, adapisoricids, or geolabidines.

Phylogeny of the Leptictidae

Previous taxonomic arrangements of leptictids have reflected to a large extent the biostratigraphic occurrence of the various species (Douglass, 1905, Matthew and Granger, 1918, Scott and Jepsen, 1936). All Oligocene species were indiscriminantly lumped under *Leptictis (=Ictops)*. Paleocene-early Eocene forms were assigned to *Palaeictops* and early and middle Eocene forms to *Diacodon*. Van Valen (1967) attempted a more phyletic arrangement of species and his results show some strong departures from previous classifications. Van Valen specified that his study was only preliminary and accordingly did not present rigorous definitions of the leptictid genera and species he considered. Further, he did not attempt to subdivide Oligocene leptictids into major lineages but noted that such a revision might be in order. It is evident that there are at least two major groups of Oligocene leptictids which can easily be separated at the generic level (Novacek, 1976). One of these (now being studied by the author) shows phyletic relationships with *Prodiacodon*. The second group is represented by *Leptictis haydeni*, *L. dakotensis*, *L. douglassi*, and perhaps *L. wilsoni* (Novacek, 1976) and is most clearly related to *Palaeictops*, particularly *P. matthewi* and *P. multicuspis* from the dental and cranial similarities noted above. Thus the basic dichotomy seen in Oligocene forms might be traced as far back as the Paleocene.

Fig. 14 is a graphic representation of the hypothesized phylogeny of the Paleocene and Eocene North American Leptictidae. The numbers given at each node of the branches refer to proposed shared-derived (synapomorphic) characters which unite the groups stemming from them. The following characters separate leptictids from *Gypsonictops*:

1. Four lower premolars.
2. Narrow stylar shelves.
3. Hypocones uniformly present on upper molars
4. $P_{\overline{5}}$ with a well developed paraconid.
5. Entoconulid present on $M_{\overline{3}}$.

Recognition of the above characters as derived is based on interpretations of early therian dental evolution. Five premolars are variably present in *Gypsonictops* and *Kennalestes* and most likely represent a plesiomorphous condition in Eutheria (McKenna, 1975). All Tertiary leptictids (where complete postcanine dentitions are known) have only four premolars and, in agreement with McKenna (1975), it is hypothesized that they represent a derived evolutionary stage through loss of $P\frac{2}{3}$. Characters 2 and 3 stem from the generally accepted conclusion that eutherians evolved from a primitive condition where the upper molars had wide stylar shelves and lacked hypocones (Patterson, 1956; Slaughter, 1965, 1971; Crompton, 1971; Fox,1975). In *Gypsonictops* the hypocone is vestigial or absent, and the stylar shelves are wider than in Tertiary leptictids. $P_{\overline{5}}$ paraconids (character 4) are absent or small in *Gypsonictops*, but well developed in Tertiary leptictids. The polarity of this character is difficult to determine. Paraconids on the last premolar are uniformly lacking or weakly developed in a number of early primitive eutherians including *Kennalestes* (see Kielan-Jaworowska, 1969). However the paraconid is large in the $P_{\overline{5}}$'s of *Procerberus* (see Lillegraven, 1969). It is tentatively argued here that a $P_{\overline{5}}$ with a very small (or absent) paraconid is primitive for eutherians but this feature may prove to be a derived specialization of *Gypsonictops*. Entoconulids on the $M_{\overline{3}}$ (5), a feature common to primitive species of *Prodiacodon* and *Myrmecoboides montanensis* but absent in *Gypsonictips*, is presumed to represent a derived character uniting Tertiary leptictids. It must be noted that certain other Cretaceous eutherians have lower molar entoconulids (e.g. *Cimolestes magnus*, see Lillegraven, 1969).

Myrmecoboides montanensis can be separated from all other leptictid clades by three unique specializations in the lower dentition:

6. Closely appressed metaconids and paraconids, producing a "twinning" effect of these two cusps.

7. Anteroposteriorly elongated talonids.

8. Widely spaced anterior premolars.

Although the isolated phyletic position of *Myrmecoboides* within the Leptictidae seems clear, it is not certain whether the divergence of this lineage occurred before or after the *Palaeictops-Prodiacodon* dichotomy.

Prodiacodon is the most primitive leptictid genus and does not show many derived characters other than those recruited to unite all members of the family. One possible derived character unique to *Prodiacodon* is the "doubled" paraconule (9) in the upper molars of *P. Puercensis, P. crustulum,* and *P. tauricinerei.* Definitely referable upper molars are not known in *P. furor* and *P. concordiarcensis.*

Palaeictops is regarded here as the most derived genus among the Paleocene-Eocene leptictids known from North America, distinguished by the following specializations:

10. P^{5}'s and upper molars are more "bunodont", being more anteroposteriorly elongate and transversely compressed, with lower, more bulbous paracones, metacones, and protocones.

11. Parastylar spurs M^{2-3} are not prominent and ectoflexi are not deep.

12. Hypocones are well developed, being more than half the height of the protocones.

13. Conules are situated labially at the base of the paracone and metacone.

14. Molar trigonids are not greatly elevated.

15. P_{5} paraconids are well developed.

16 Paracone on P^{4} is moderately to greatly enlarged.

17. Tibia and fibula are fused for most of their shaft lengths.

The central hypothesis argued in this study is that the sectorial features in the molars of *Prodiacodon*, namely high, piercing molar cusps on transverse molars with salient parastylar spurs, represent a primitive leptictid condition. This conclusion stems from the acknowledgment of the distribution of "sectorial" dental features among palaeoryctids, leptictids, and Cretaceous Mongolian eutherians. *Palaeictops* is removed from this condition in characters 10, 11, and 14 above. The derived

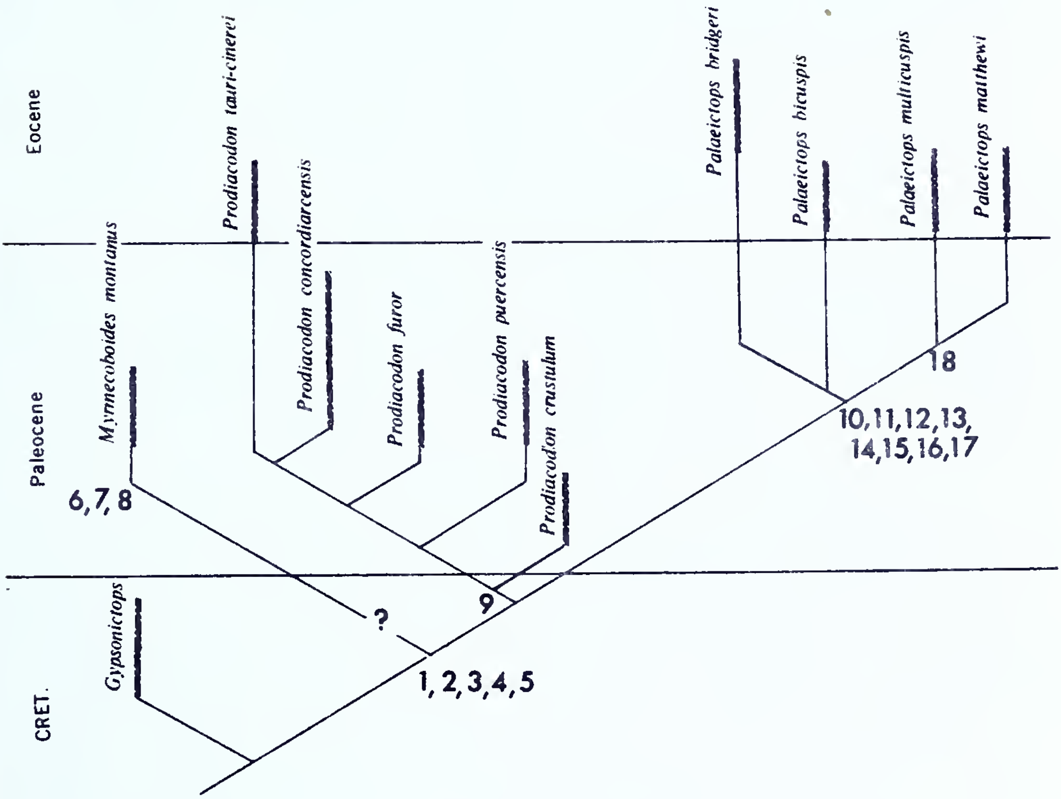

FIG. 14. Postulated phylogenetic relationships of the North American Paleocene and Eocene Leptictidae. Vertical bars with diagonal stripes represent the approximate geochronological occurrence of a particular taxon. The intersections of branches are only meant to reflect the relative sequence of splitting. The time of branching on a geochronologic scale is not intened to be represented here. Numbers refer to shared-derived characters discussed in the text.

states represented by characters 12 and 15 are recognized as tendancies for increased development of molar hypocones and $P_{\overline{5}}$ paraconids already present in the most primitive leptictids. The labial position of the upper molar conules in *Palaeictops* (character 13) represents a distinct departure from that in *Prodiacodon*. The lingual position of upper molar conules in *Prodiacodon* is recognized as a primitive condition for the Eutheria (Patterson, 1956; Slaughter, 1965, 1971; Turnbull, 1971; Fox, 1975). Enlargement of the $P^{\underline{4}}$ paracone (16) in *Palaeictops* is variable. The $P^{\underline{4}}$ paracone is distinctly enlarged in the Oligocene *Leptictis*. Character 17 is shared by *Palaeictops* (where known) and the Oligocene *Leptictis*, but the tibia and fibula are unfused in *Prodiacodon*.

Palaeictops multicuspis and *P. matthewi* are synapomorphic in the enlargement and proliferation of cusps on $P_{\bar{4}}$ (character 18).

An effort was made to establish a phylogenetic scheme without reference to the age and occurrence of a particular taxon, but as is clearly demonstrated by Fig. 14 there seems to be little discrepancy between the hypothesized phylogenetic relations of taxa and the recorded age of their occurrence. Primitive species of *Prodiacodon* are recorded as far back as the early Paleocene, the new Puercan species *P. crustulum* showing dental characters intermediate between the late Cretaceous *Gypsonictops* and middle Paleocene species of *Prodiacodon*. Medial and later Eocene species of *Palaeictops* show the closest resemblance to the Oligocene *Leptictis*. There are, of course, exceptions (e.g. *Myrmecoboides, Prodiacodon concordiarcensis*) and these are interpreted as early divergently specialized lineages.

Although a number of major changes in leptictid taxonomy at the generic level have been proposed in this study, the overall number of species has not been reduced. I do not feel that this result is due directly to a subliminal desire on my part to "over split", but is a reflection of true diversity. Many of the species described above are represented by only one or two specimens but I doubt that larger referable samples and a better idea of dental variation would serve to unite these taxa, as the cited differences between them are generally very distinct. In the cases where larger samples of leptictids are available (e.g., *Leptictis dakotensis* from the Oligocene of North America) the variation in important comparative dental characters is clearly not great. Leptictids evidently were quite diverse, at least at the species level, throughout their Tertiary history.

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A NEW GENUS OF MURID RODENT FROM THE MIOCENE OF PAKISTAN AND COMMENTS ON THE ORIGIN OF THE MURIDAE

by

LOUIS L. JACOBS[1]

ABSTRACT

Antemus chinjiensis, new genus and species, from middle Miocene Siwalik deposits of Pakistan is the oldest and most primitive member of the Muridae yet described. It confirms that murids evolved from the Cricetidae and allows determination of homology of upper molar cusps. The present centers of diversity of the Muridae are the result of emigration from a south Asian center of origin no earlier than Miocene time.

INTRODUCTION

Rodents of the family Muridae, commonly referred to as Old World rats and mice, are among the most diverse and successful of all living groups of mammals. Although their distribution is essentially world-wide, they presently have three distinct centers of diversity: southern Asia, Africa south of the Sahara, and the Malay Archipelago, plus Australia and New Guinea. Students of evolution, biogeography, and systematics have been unable to evaluate the significance of these centers of diversity satisfactorily because of lack of paleontological evidence as to the time and place of origin of the family. Thaler (1966) suggested that the group evolved in the Eocene of tropical Asia, and James and Slaughter (1974) interpreted the known fossil record of murids in the circum-Mediterranean region as indicating a Miocene origin of the group in southern Europe. These hypotheses are untenable on paleontological grounds because the oldest previously described murid, *Progonomys*, from the late Miocene (Vallesian) of Europe (Michaux, 1971) exhibits typical murid morphology and, therefore, sheds little light on the origin of the group.

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Recently a small sample of murid teeth was recovered from the type Chinji Formation of the Siwalik Group, Pakistan. The type Chinji is considered middle Miocene, possibly Astaracian (Fahlbusch, 1976) equivalent, because the three-toed horse, *Hipparion*, a North American immigrant first occurring in Europe in the late Miocene (Vallesian), occurs only above the Chinji Formation in the Siwalik Group (Simons, Pilbeam, Boyer, 1971). Recent study of other large mammal taxa from the type Chinji Formation by D. Pilbeam and associates also indicates a pre-Vallesian age (D. Pilbeam, personal communication). If correlations based on *Hipparion* and other large mammals are correct, the Chinji specimens represent the oldest known member of the family Muridae. In addition, the morphology of the Chinji murid, as described below, indicates that murids evolved from the Cricetidae, hamsters and their relatives, and allows conclusive interpretation of homology of murid upper molar cusps with those of the Cricetidae and most other mammals. Thus, the geographic and chronologic occurrence of the Chinji murid, along with its primitive dental morphology, suggests that murids originated in the Miocene of southern Asia.

The most recent discussions of the origin of murids (Petter, 1966; Vandebroek, 1966; Lavocat, 1967) utilize arrangements, or seriations, of dental morphotypes (see Simpson, 1975) of known fossil and Recent taxa. The taxa used in these seriations often have little genetic affinity, and temporal (stratigraphic) successions, necessary to demonstrate ancestor-descendant relationships, have not been realized. The difficulty in determining the origin of murids stems from the unique structure of their upper molars (Fig. 1A, B, and 2), even though the structure of the lower molars of murids suggests a relationship to cricetids. The upper molars consist of transverse rows (hereafter referred to as chevrons and numbered from anterior to posterior; *e. g.*, the anterior chevron on M^1 is the first chevron) comprising three tubercles in the first and second chevrons of M^1. The third chevron of M^1 in known early forms (and many later forms) has only two tubercles.

Attempts at interpreting homology of cusps with other groups of rodents have been inadequate. In order to discuss the upper teeth, Miller (1912) devised a scheme in which each tubercle from lingual to labial side is designated by number (*e. g.*, the cusps on the first chevron are t_1, t_2, t_3; on the second chevron, they are t_4, t_5, t_6). This scheme has been modified by various authors (Michaux 1971; Misonne, 1969). I accept Michaux's modification of Miller's scheme and refer to the transverse rows as "chevrons" for convenience in describing murid upper molars. There is no problem in determining homologies for cusps on lower molars of murids because they exhibit rather straightforward modifications of the characteristic cricetid plan.

Murid genera, both fossil and living, can almost always be identified on the basis of molar structure (Misonne, 1969; Lavocat, 1962), and phylogenetic interpretations have been based upon molar morphology (Michaux, 1971). Therefore, a discussion of the origin of murids based on the Chinji specimens is justified, even though the present sample size is small.

SYSTEMATICS

Order Rodentia

Family Muridae

Subfamily Murinae

Antemus chinjiensis, new genus and species

(Figure 1)

Holotype: Geological Survey of Pakistan 7649, M^1.

Age: Middle Miocene.

Distribution: Presently known from Yale:GSP locality 41, type Chinji Formation, Punjab, Pakistan.

Hypodigm: GSP 7649, 7650 M^1, 7651 M^2, 7652 M_2.

Diagnosis: Murid rodent with t_4 on M^1 and M^2 isolated; no t_1 on M^2; t_6 and t_9 well separated; t_4 not joined to t_8; valley between t_1 and t_4 shallow, similar in depth to the valley between t_4 and t_8; labial cingulum on M_2 weak.

Etymology: Generic name from *ante*-, a prefix meaning before in time, and *mus* (Latin, masculine); specific name for Chinji, plus -*ensis* (Latin), a suffix denoting place.

Description: *Antemus* is known from four isolated cheek teeth ($2M^1$, $1M^2$, $1M_2$), all from the same locality. The cheek teeth are brachydont with rounded and distinct cusps. The cusps slant slightly posteriorly on M^{1-2}, anteriorly on M_2. The two M^1 are in slightly different stages of wear, but exhibit the same occlusal pattern, and obviously belong to the same taxon. The M^2 has an occlusal pattern identical in basic respects to that of M^1, except that the anterior portion of M^1 (t_2 in this case) has no homolog on M^2. This is the usual condition in muroid rodents. The M_2 is referred to *Antemus* because it has a murine pattern and is slightly narrower than M^2. The width of M^2 (GSP 7651) relative to width of M_2 (GSP 7652) is similar to the ratio of the width of second molars in individual species of *Progonomys* (see measurements in Michaux, 1971, and Van de Weerd, 1976). Muroid rodents associated with *Antemus* at this locality are the cricetids *Megacricetodon* sp. and *Copemys (Democricetodon)* sp. The dentitions of these taxa are well known and quite distinct from *Antemus*.

M^1 (Fig. 1A, less worn; and 2, more worn) exhibits the basic murine pattern of three transverse chevrons. The first chevron is

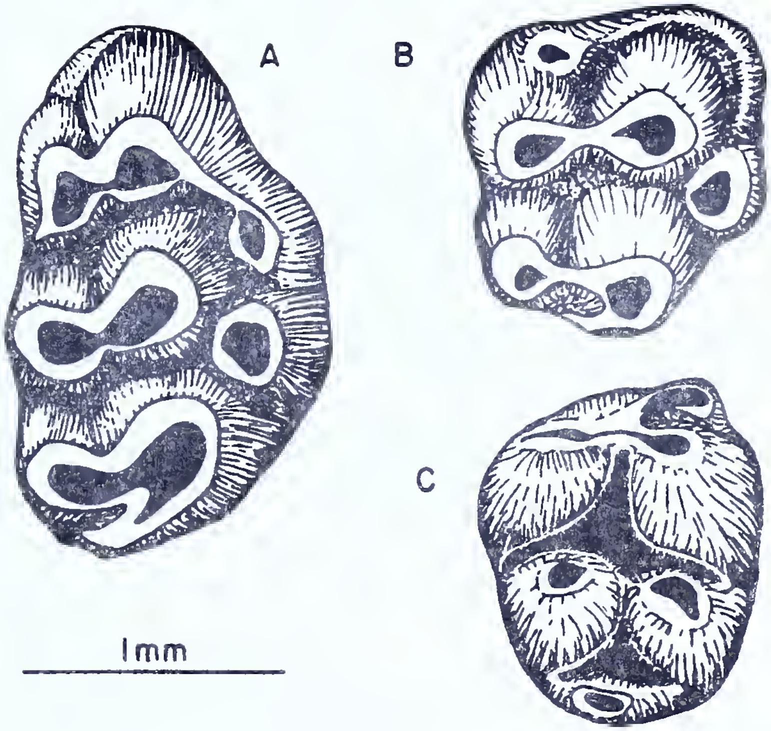

Figure 1. *Antemus chinjiensis*. A. Right M^1 (GSP 7649, holotype, length = 1.90 mm, width = 1.20). B. Right M^2 (GSP 7651, length = 1.20, width = 1.10). C. Right M_2 (GSP 7652, length = 1.25, width = 1.05).

formed by three connected cusps (t_1, t_2, t_3 from lingual to labial side). The second chevron includes three cusps (t_4, t_5, t_6). The third chevron has only two cusps (t_8, t_9). There is no trace of t_7. A narrow posterior cingulum extends labially from t_8. The t_1 is posterior to t_2 and t_3; t_1 is well developed, but small in relation to t_2. A thin, distinct ridge joins the anterior margin of t_1 to the posterolingual margin of t_2. The t_2 is the largest cusp in the first chevron and is about equal in size to t_5 and t_8; it is joined to the t_3 by a posterior crest. The t_3 is about the size of t_1. The t_4 is fairly large, rounded, and isolated. It is slightly posterior to t_5 at the lingual edge of the valley separating the second from the third chevron, but is more closely associated with the second chevron than the third. The t_4 is separated from t_1 and t_8 by shallow valleys. The t_5 is the largest cusp in the second chevron; it is joined to the t_6 only by a posterior crest (rather than by anterior and posterior crests as in some cricetids). The t_6 is smaller than t_4. Cusps t_8 and t_9

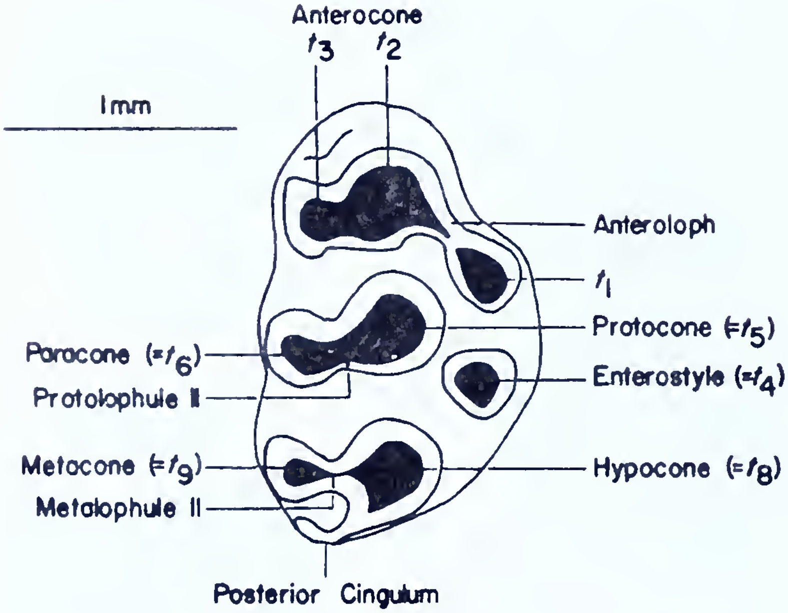

Figure 2. *Antemus chinjiensis* right M^1 (GSP 7650, length = 1.75 mm, width = 1.15). Cusp terminology after Wood and Wilson (1936), and Michaux (1971).

connect posteriorly, and t_8 is larger than t_9. The posterior cingulum is ridge-like, becoming broader with wear, and extends from the posterolabial margin of t_8 to a point behind and slightly labial to the midline of t_9. A minute stylar cusp is located at the base of juncture between t_2 and t_3 at the anterior edge of the tooth. There are no other accessory cusps, styles, or lophs. Three roots are present on M^1.

M^2 (Fig. 1B) has four basic cusps (t_5, t_6, t_8, t_9) forming two rather poorly defined chevrons. The t_5 and t_6 are weakly connected slightly posterior to their transverse midline and form the anterior chevron. Cusps t_8 and t_9 are similarly weakly connected and form the posterior chevron. The posterior cingulum extends labially from t_8. There is no t_1; instead, there is a prominent cingulum which extends posteriorly from the anterolingual corner to the middle of the lingual margin of the tooth. There it joins a well developed t_4 which is situated at the lingual side of the transverse valley between the chevrons. The t_4 is isolated from either chevron. The t_3 is small and is located at the anterolabial corner of the tooth. There is no trace of t_2, t_7, or other accessory cusps, styles or lophs. The roots are not preserved on this specimen.

A single, slightly corroded, M_2 (Fig. 1C) of *Antemus* is known. It comprises four main cusps (protoconid, metaconid, hypoconid, and entoconid). The labial cusps are placed slightly posterior relative to the lingual cusps. Protoconid and metaconid are weakly connected anteriorly, as are the hypoconid and entoconid. The posterior cingulum is transversely compressed and extends along the posterior margin of the tooth between the hypoconid and entoconid. The labial anteroconid is low, but well developed, on the anterior cingulum. The labial cingulum is weak and indistinct.

Comparisons: The presence of three cusps in the first and second chevrons of M^1 with t_1 involved in the first chevron and t_4 associated with the second chevron indicate the murid affinity of *Antemus*. *Antemus* differs from all known Tertiary murids in having no t_1 on M^2. *Antemus* resembles *Progonomys* (see Michaux, 1971, and Van de Weerd, 1976) in being brachydont with distinct but weakly connected cusps. These are apparently primitive characters which are modified in more derived forms. *Antemus* is further distinct from *Progonomys* in having a much weaker labial cingulum on M_2. The M^1 of *Antemus* is distinct from that of *Occitanomys* (Michaux, 1969) in being less stephanodont, that is, the chevrons in *Antemus* are well separated and are not connected at t_6-t_9 or t_4-t_8 nor is a spur directed from either the t_1 or t_3 toward t_5.

Antemus resembles some specimens of *Progonomys hispanicus* and *Occitanomys* in having isolated t_4 on M^1, but the isolation of t_4 in *P. hispanicus* and *Occitanomys* is a variable character (Van de Weerd, 1976) and not diagnostic for either *P. hispanicus* or *Occitanomys*. Data given by Van de Weerd (1976) indicate that the occasional isolation of t_4 on M^1 in these taxa is convergent with the condition seen in *Antemus*. Even in these cases of similarity, the lower-crowned nature of the M^1 of *Antemus* marks it as more primitive; the shallowness of the valley between t_1 and t_4, relative to that between t_4 and t_8 and in comparison with similar variations of *Progonomys* and *Occitanomys*, easily reveals this difference.

ORIGIN OF THE MURIDAE

The Muridae have long been considered closely related to the Cricetidae (Miller and Gidley, 1918; Simpson, 1945; Wood, 1955) because of skull structure, dental formula, and lower molar morphology. The murids are distinct from cricetids in having three longitudinal rows of cusps in the upper molars with t_1 involved in the first chevron and t_4 involved in the second chevron. Because no fossil intermediates between the two families have been described, no satisfactory explanation has been given as to which row of cusps was added in the murid dentition. Consequently, the homology of cusps in upper molars of cricetids and murids has not been demonstrated and several patterns of homology have been suggested or implied (see, for instance, Thaler, 1966; Vandebroek, 1966; Schram and Turnbull, 1970).

Vandebroek (1966) considered that the central row of cusps (t_2, t_5, t_8) was added in the murid dentition. His theory traces the ancestry of murids back through a sigmodont stage to a *Theridomys* stage. Lavocat (1967) strongly criticized Vandebroek's theory. There is at present no evidence which supports any close relationship between murids and sigmodonts or theridomyids, or, for that matter, between sigmodonts and theridomyids.

Other authors (*e.g.*, Thaler, 1966; Miller and Gidley, 1918; Schaub, 1938; Petter, 1966) considered that the lingual row of cusps (t_1 and t_4)was added. Petter (1966) suggested that a seriation, or arrangement of forms, including *Cricetodon*, *Petromyscus*, *Dendromus*, *Cricetomys*, and *Parapodemus* illustrates progressive development of a lingual row of cusps and loss of longitudinal connections between cusps. This seriation was presumed to demonstrate stages through which murids evolved. Petter's theory was modified by Lavocat (1967) to include *Myocricetodon.*

The most serious objections to Petter's theory concern the lingual cusps and how they are associated with chevrons. *Cricetomys* usually has two lingual cusps; however, the anterior lingual cusp is associated with the second chevron, while the posterior lingual cusp is associated with the third chevron. In murids, the t_1 is associated with the first chevron and t_4 with the second chevron. Sen (1975) suggested that the murid *Euxinomys galacticus* from the Pliocene of Turkey is similar to Petter's *Cricetomys* stage because the t_1 is connected to the t_5 and not t_2. However, *Euxinomys* is strongly stephanodont, that is, cusps are connected at t_1-t_5, t_3-t_5, t_4-t_8, and t_6-t_9. It seems most likely that the connection between t_1 and t_2 is lost secondarily as in some specimens of *Occitanomys* (Van de Weerd, 1976).

In all previously described Tertiary murids, and most modern murids, the anterolabial border of t_4 is connected to the posterolingual border of t_5. *Myocricetodon* and *Dendromus* have only one lingual cusp, and it is associated with the second chevron. However, the lingual cusp in *Myocricetodon* is connected to the posterolabial border of the protocone, a condition never observed in the Muridae. In *Dendromus,* the posterior border of the lingual cusp joins the posterior border of the protocone. *Petromyscus* also has one lingual cusp, but Petter (1967) considers it the protocone and distinguishes the Petromyscinae because a new cusp is added between the protocone and paracone. The protocone shares a posterior connection with the new cusp in petromyscines. *Myocricetodon*, *Dendromus,* and *Petromyscus* are thus excluded from the ancestry of the Muridae.

All known Tertiary murids have a t_1 on M^2, except for *Antemus* which has an anterior cingulum. Cricetids have no t_1 on M^2, but they also have an anterior cingulum. *Antemus* is similar to cricetids with respect to this character. Therefore, the lack of t_1 on M^2 in *Antemus* is a primitive character which is modified in later murids. The development of t_1 from an anterolingual cingulum on M^2 implies that the t_1 on M^1 and t_4 on M^{1-2} in murids were also derived from cingula.

It is somewhat anomalous that the t_4 in *Antemus* is isolated, whereas the t_1 on M^1 is connected to t_2. However, the connection of t_1 and t_2 in the M^1 of *Antemus* is consistent with the hypothesis that the t_1 developed on the anterior cingulum. In the M^1 of cricetids, the anterior cingulum extends from the anterocone. If an additional cusp developed on the anterior cingulum, as proposed here, it would be connected to the anterocone. The t_4 is apparently the only cusp which developed on a lingual cingulum. Its isolation is considered a primitive character. Later murids share the character of t_4 connected to t_5, except in those forms (*e. g.*, some specimens of *Occitanomys* and *Progonomys hispanicus*) where the connection is secondarily lost (Van de Weerd, 1976).

Thaler (1966) observed that the posterior cingulum in murids, which he called t_{12}, originates from t_8. In other rodents, including cricetids, the posterior cingulum originates from the hypocone. This is strong evidence that the murid t_8 is homologous with the hypocone. *Antemus chinjiensis* is significant, because of its transitional form, in confirming the homology of cusps in murid dentitions with those of cricetids and most other mammals.

The first chevron of the murid M^1 comprises the cricetid anteroloph and bilobed anterocone. The t_1 is a neomorph developed on the anteroloph with no counterpart in the cricetid molar. The t_2 is the lingual lobe of the anterocone, and t_3 is the labial lobe. In the second chevron, t_4 is the enterostyle of Wood and Wilson (1936), t_5 is the protocone, and t_6 is the paracone. Protocone and paracone are connected by protolophule II. The third chevron of the murid molar comprises t_7, t_8, and t_9. The t_7 is absent in known early forms and variously present or absent in later forms; when present, it is a neomorph with no cricetid homolog. The t_8 is the hypocone; t_9 is the metacone. Hypocone and metacone are connected by metalophule II. On the murid M^2, the t_1 and t_3 are developed from the anterior cingulum. As there is no anterocone in the cricetid M^2, there is no chevron on the murid M^2 which corresponds to the first chevron on M^1. Other structures on M^1 are as labeled in Figure 2.

Murids probably evolved from a cricetid ancestor which possessed an M^1 with a strongly bilobed anterocone and a posterolingual extension of the anterior cingulum. Further dental modifications involved in the evolution of murids from cricetid ancestors are: (i) reduction or loss of accessory lophs; (ii) development of a posterior connection only between protocone and paracone and between hypocone and metacone; (iii) development of t_1 from the anterior cingulum; (iv) development of enterostyle from a lingual cingular shelf.

Emry and Dawson (1972) suggested that the early Oligocene cricetid *Nonomys* might be related to the Muridae because it has cuspate lower molars with well developed labial cingula. The M_2 of *Antemus* does not have a well developed labial cingulum, and, therefore, suggests that the ancestor of murids did not have well developed labial cingula. While no upper molars of *Nonomys* are known, it appears unlikely that *Nonomys* is directly related to murids.

There is no presently known cricetid which can be considered directly ancestral to the Muridae. However, the ancestral form will probably be found in the Cricetinae or Cricetodontinae (*sensu* Mein and Freudenthal, 1971). Both subfamilies contain genera with bilobed anterocones and relatively simple upper molars. In general, the Cricetinae appear too specialized. I suspect that the cricetid ancestor of murids is a south Asian Miocene cricetodontine, perhaps somewhat similar to *Megacricetodon*.

DISTRIBUTION

If the correlation of the type Chinji Formation with the European sequence suggested in the introduction is correct, *Antemus* is older than any other murid yet discovered. Numerous localities in Europe, Africa, and North America of the same age or older than type Chinji have yielded abundant rodent fossils, but no murids. The occurrence of *Antemus* in Miocene beds of the Indian subcontinent implies that murids originated in southern Asia, probably in the early or middle Miocene. Adaptive radiation then occurred in Asia, giving rise to the present day south Asian center of murid diversity, including the genera *Rattus* and *Mus*.

Early in their history, but certainly by late Miocene, murids spread to the circum-Mediterranean region and evolved into several genera, including *Apodemus*. Some elements of the circum-Mediterranean murid fauna migrated south, no earlier than late Miocene or early Pliocene, and there radiated into the diverse murid fauna living today in subsaharan Africa.

The history of the murid fauna of the Malay Archipelago, Australia, and New Guinea is much more complex, and probably involved multiple invasions by island hopping, resulting in numerous endemic genera. Regardless of number of invasions, the initial introduction of murids into this region occurred, as suggested by Simpson (1961), no earlier than Miocene.

Murids have entered North America only where influenced by man. Modern distribution of murids, and their fossil distribution, suggest a strong preference for warm climate. Murids were probably prevented from crossing the Beringian connection between Asia and North America by cooler temperature.

Thus, one of the most successful families of mammals is also one of the latest to evolve. The Muridae have had a complex, albeit relatively short, history of immigration followed by radiation resulting in the present distribution and diversity of the family.

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A NEW SPECIES OF *GREGORYMYS* (RODENTIA, GEOMYIDAE) FROM THE MIOCENE OF COLORADO

by

JENS MUNTHE[1]

ABSTRACT

Gregorymys larsoni n. sp. is a very late survivor of the *Gregorymys* lineage. It is known only from the Derby Peak fauna of late Barstovian or early Clarendonian age. Radiometric dates obtained from volcanic rocks above and below the sediments from which the Derby Peak fauna was collected range from approximately 13 to 10 million years before present. *G. larsoni* is temporally disjunct from all previously described species of the genus and may represent a population surviving only within a persistent refugium.

INTRODUCTION

A small collection of mammals was obtained from Derby Peak in Garfield County, Colorado by a University of Colorado party in 1967. The geology of the area was studied in subsequent years and radiometric ages were determined for rocks above and below the fossiliferous sediments. Because the stage of evolution of one of the rodent taxa represented in the collection appears anomalous with respect to the remainder of the fauna and the radiometric dates, this rodent was studied in detail to determine its affinities. It is described here as a new species and the geologic and faunal evidence bearing on the age of the deposit is discussed.

Measurements of the holotype were made with an EPOI Measuring Microscope and are shown in Table 1. Acronyms used are AMNH (= American Museum of Natural History), CM (= Carnegie Museum), FMNH (= Field Museum of Natural History), UCM (= University of Colorado Museum), and UCMP (= University of California Museum of Paleontology).

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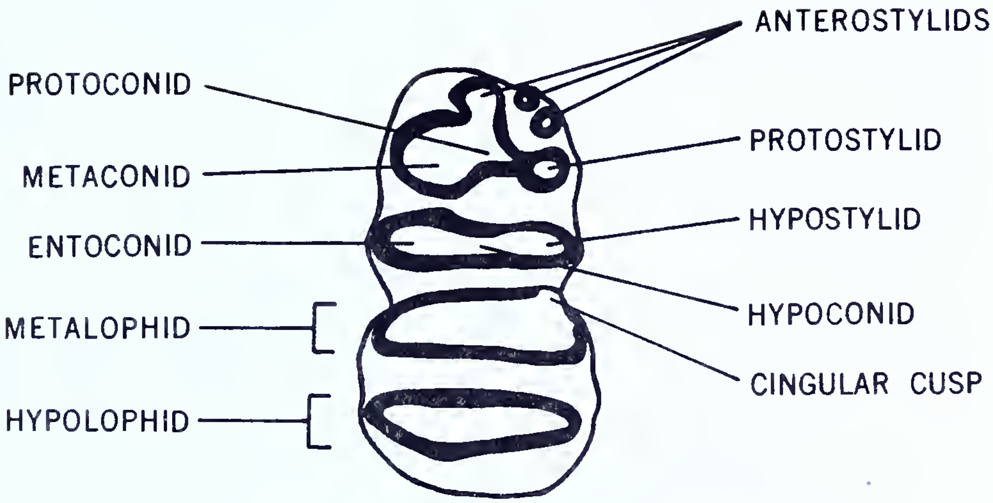

Figure 1. Cheek tooth cusp terminology for *Gregorymys larsoni*. The major metalophid and hypolophid cusps occupy the same relative positions on the molars as on P_4.

The cheek tooth cusp terminology employed here (Fig. 1) is that of Rensberger (1971:110). The terminology for P_4, however, is used only in a topographic sense. Cusp homologies are not implied. If *Gregorymys* is ultimately descended from *Heliscomys*, which had only three cusps on P_4, then one of *Gregorymys'* principal cusps is a neomorph not homologous with the four principal cusps of generalized rodent teeth. Several attempts have been made to homologize geomyoid P_4 cusps assuming that *Heliscomys* had lost one principal cusp (*e. g.*, Shotwell, 1967; Lindsay, 1972), but none of these is entirely satisfactory. I have therefore used names topographically for simplicity and clarity.

SYSTEMATICS

Superfamily Geomyoidea Weber, 1904

Family Geomyidae Gill, 1872

Subfamily Entoptychinae Miller and Gidley, 1918

Gregorymys Wood, 1936

Gregorymys larsoni new species

(Figure 2)

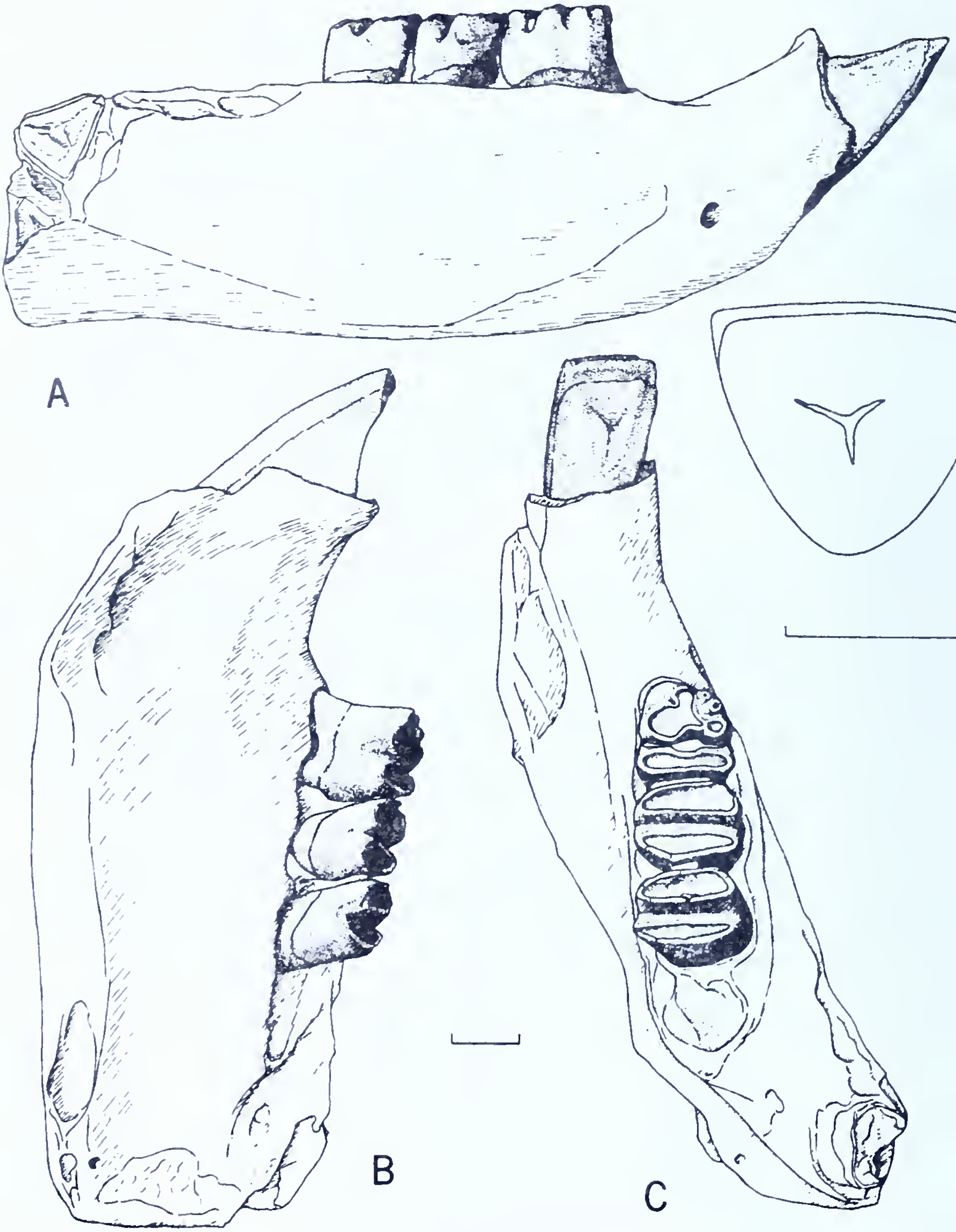

Figure 2. *Gregorymys larsoni* n. sp., UCM 29745. A. Lateral view. B. Lingual view. C. Occlusal view. D. Cross-section of incisor. Scale bars equal 1 mm.

Holotype: UCM 29745, right mandibular ramus with I-M_2.

Hypodigm: Type only.

Etymology: Patronym for Dr. Edwin E. Larson, who discovered the type locality and has been instrumental in deciphering the Cenozoic history of the area.

Locality: UCMP locality V76111, Derby Peak, Garfield County, Colorado. Detailed locality information may be obtained from the Museum of Paleontology, University of California, or the University of Colorado Museum.

Age: Late Barstovian or early Clarendonian.

Diagnosis: Very small species of *Gregorymys* (Table 1); mandible shallow (Table 1); diastema short (Table 1); protoconids and hypoconids weakly developed.

Description: The mandible is shallow for the genus. Its depth is 70% of P_4-M_3 length as opposed to 83% in AMNH 12895, referred by Wood (1936) to *G. curtus*, and 107% in CM 8999, the type specimen of *G. kayi* (Wood, 1950). The diastema is shallow and much shorter than in any previously described specimen of *Gregorymys*. Its length is less than half the P_4-M_3 length, whereas the diastema is approximately two-thirds as long as the cheek tooth row in FMNH 12221, the type specimen of *G. riggsi* (Wood, 1936) and CM 8999. The masseteric crest is low but sharply defined. It extends in a smooth arc from below the posterior portion of the diastema, immediately posterior to the small mental foramen, to a point below the hypolophid of M_2. A weak, rounded crest begins at the posterior end of the masseteric crest and follows the ventral margin of the incisor alveolus into the ascending ramus. This is distinctly different from the condition in AMNH 12895, where the masseteric crest is sharply angled and there is no crest posterior to it along the incisor alveolus. The angle is missing, but it extended anteriorly as far as M_3. The symphysis is rugose. A shallow genioglossal fossa lies immediately posterior to its dorsoventral midpoint. A narrow ventrolingual crest, presumably the area of insertion of M. digastricus, extends from the symphysis to a small ventral process below P_4. A rugose swelling near the ventral margin of the mandible below the hypolophid of P_4 may have been the area of origin of M. transversus mandibulae. A similar swelling occurs in some specimens of *G. curtus*. The prominent chin process seen in some specimens of *G. curtus* is lacking.

P_4 has three anterostylids, of which the most lingual is the largest, arranged in an arc anterolinguad of the metalophid. The lingual anterostylid differs from that in other described specimens of *Gregorymys* in its greater size and more labial position. In this respect it most closely approaches the type specimen of *G. riggsi*. The metalophid has only a very weak protoconid that has not yet united with the protostylid. The hypolophid has equally developed entoconid and hypostylid but a weak hypoconid. The posterior margin of the hypolophid is straight, in contrast to the more arcuate hypolophids of other specimens, particularly AMNH 12909, referred to *G. formosus* by Wood (1936) and to *G. curtus* by Macdonald (1970). With increased wear a small enamel lake would develop between the anterostylids and the metalophid as in AMNH 12909. At a still later wear stage, a lake would form between the metalophid and hypolophid as they would unite first labially and then lingually. This is a result of the weak development of the central cusp in each of these lophids.

M_1 and M_2 also show weak development of the protoconid and hypoconid in contrast to other species of the genus. The cingular cusp of the metalophid is slightly lingual to the protostylid, causing the labial margin of the metalophid to lie oblique to the anteroposterior axis of the tooth row on both M_1 and M_2. This is typical of M_2 in other species of *Gregorymys*, but in most previously described specimens the anterolabial cusp and protostylid are equally labial on M_1. With increased wear the metalophids and hypolophids would unite medially and labially at almost exactly the same time. A very short-lived enamel lake would thus be formed on the labial half of the tooth. The lophids would then unite progressively more lingually. The lophid unions in FMNH 12221 (*G. riggsi*) would be similar, although in that specimen the first connection is definitely at the labial margin and the medial connection is slightly linguad of that in *G. larsoni*. In all other species, the valley between the lophids is very deep in the center of the tooth so that a persistent central enamel lake is formed.

Cement is present around the roots and slightly above on P_4 and it extends well up on the crowns of M_{1-2}, particularly labially. This development of cement exceeds that seen in specimens of *G. curtus*, is very similar to *G. riggsi*, and is less than in *G. douglassi* (Wood, 1936) and *G. kayi* (Wood, 1950).

The lower incisor is broad, flat anteriorly, and triangular in cross-section. The enamel is thin and is almost entirely confined to the anterior surface. The triradiate pulp cavity is identical to that in AMNH 12895 (*G. curtus*). The root is not preserved, but the incisor extended posterodorsally at least above the occlusal surfaces of the cheek teeth. The incisor is larger relative to the cheek teeth than in any other species of *Gregorymys* (Table 1).

Discussion: Certain aspects of geomyoid superspecific taxonomy are fundamental to an understanding of *G. larsoni's* relationships to other members of this superfamily. Shotwell (1967:10) included the subfamilies traditionally grouped as Geomyidae within Heteromyidae. Rensberger (1971:151) advanced additional reasons for this arrangement and acknowledged the probable artificiality of the geomyid-heteromyid dichotomy, but retained the dichotomy in order to emphasize "the fossorial attributes of the Entoptychinae and Geomyinae" (1971:66). However, a recent study of the skeleton

Table 1. Measurements (in millimeters) of *Gregorymys larsoni* and selected comparative measurements of other species.

Measurement	UCM 29745 *G. larsoni*	AMNH 12895 *G. curtus*	FMNH 12221 *G. riggsi*	CM 8999 *G. kayi*
P_4-M_3 alveolar distance	6.60	8.10	7.45	7.80
P_4 anteroposterior (occlusal)	1.52	----	----	----
transverse metalophid	1.47	----	----	----
transverse hypolophid	1.60	----	----	----
M_1 anteroposterior (occlusal)	1.33	----	----	----
transverse metalophid	1.64	----	----	----
transverse hypolophid	1.62	2.31	2.39	2.30
M_2 anteroposterior (occlusal)	1.41	----	----	----
transverse metalophid	1.60	----	----	----
transverse hypolophid	1.66	----	----	----
M_3 anteroposterior (alveolus)	1.24	----	----	----
transverse (alveolus)	1.29	----	----	----
I anteroposterior	1.42	----	----	----
transverse	1.53	1.75	1.96	1.99
anteroposterior/ transverse	0.928	----	----	----
enamel thickness	0.03	----	----	----
Length of diastema	3.17	7.30	5.05	5.10
Depth of mandible below P_4	4.62	6.70	6.50	8.00

of *Schizodontomys* (Munthe, 1975), an entoptychine *sensu* Wood (1936), indicates that this animal was not fossorial, but semi-saltatorial.

Gregorymys is a pivotal genus with regard to familial taxonomy of these rodents. Galbreath (1967:278-280) has summarized many of the similarities of *Gregorymys* to geomyines on one hand and heteromyines on the other. He concluded that placing *Gregorymys* in either Geomyidae or Heteromyidae might obscure its true relationships. This seems certainly to be the case even with the limited suite of morphologic characters available for comparison in this study. While its overall size, length of diastema, and size and shape of incisor argue for *G. larsoni* being a geomyid, its P_4 morphology, depth of mandible, and certain characters of the molars appear to place it in the Heteromyidae.

Despite the fact that all the above arguments support the inclusion of heteromyids and geomyids within a single family, such an arrangement is never likely to win general acceptance. Both family names are very solidly entrenched in the scientific literature. The most compelling argument against fusing the two families is the ease with which their modern representatives may be morphologically differentiated, although, as noted by Wood (1937), this morphologic disparity is largely a reflection of different habits. Neozoologists would be understandably skeptical of placing *Thomomys* and *Dipodomys* in the same family based solely on evidence provided by extinct taxa whose exact relationships to modern subfamilies are uncertain. With some misgivings, I have attempted to place *G. larsoni* within the traditional geomyoid taxonomic framework.

The subfamily assignment of *Gregorymys* to the Entoptychinae is based on its close similarity to *Entoptychus*. However, the very prominent anterior cingulum on *Gregorymys'* P_4 clearly separates it from *Entoptychus* and has led some authors (Wood, 1936:4; Shotwell, 1967:48-49) to place it closer to the heteromyines than the entoptychines in dental anatomy. Reeder (1956:411) considered *Gregorymys* to be a heteromyid and closely related to *Heteromys* on the basis of similarities in their DP_4s. The same evidence, however, was used by Hibbard (1954:357) to suggest that *Gregorymys* might be ancestral to the geomyines. Rensberger (1971), who considered more morphologic characters than any previous worker, retained *Gregorymys* within the Entoptychinae and that conclusion is followed here.

No genus other than *Gregorymys* is closely comparable to the Derby Peak specimen. The distinctive cusp arrangement of P_4, the relative sizes of the cheek teeth, the development of cement on the cheek teeth, and the broad, triangular incisor are found in combination only in *Gregorymys*. Certain heteromyines, notably some specimens of *Peridiomys* and *Diprionomys*, approach *G. larsoni's* peculiar method of uniting the lophids of P_4 more closely than previously described species of *Gregorymys*, but characters of their mandibles and especially their incisors clearly set them apart from *G. larsoni*. Similarly, the molar lophid connections of some heteromyines and some geomyines proceed as in *G. larsoni*, but characters either of the mandible and incisor or of P_4 exclude these taxa from close relationship.

In most respects, *G. larsoni* is more similar to the type of *G. riggsi* than to the other previously described specimens of the genus. None of these specimens approach *G. larsoni* in overall size, length of diastema, or depth of mandible, but *G. riggsi* is similar in P_4 morphology, sequence of lophid unification in M_{1-2}, height of crown, and development of cement.

I consider all *G. larsoni's* diagnostic characters to be derived (autapomorphies). This certainly seems to be true with respect to commonality of characters, since all other described specimens of *Gregorymys* are alike in being much larger than *G. larsoni* and having deeper mandibles, longer diastemas, and more prominent protoconids and hypoconids. *G. larsoni's* small dimensions would appear to place it in a primitive (plesiomorphic) position with respect to the other species of the genus when size trends in other groups of mammals are considered. The trend toward larger size through phylogeny is observed frequently enough to be considered an evolutionary "law", and *G. larsoni* appears to violate this law. However, some geomyoid rodents are notoriously variable in size. This is true of modern gophers and the sample of *Gregorymys formosus* studied by Macdonald (1970) is adequate to establish that it is also true of *Gregorymys*. The lengths of four P_4s from the same locality are recorded by Macdonald (1970:37) as 1.14, 1.52, 1.95, and 2.46 mm. Given this magnitude of potential variability and the unusual biogeographic circumstances under which *G. larsoni* may have evolved, its size seems less of an evolutionary anomaly, although it is presently impossible to determine whether the Derby Peak specimen is a small individual or a typical member of a dwarf taxon. It should be noted that the three dimensional diagnostic characters are probably at least partially correlated and are possibly united in a single size-dependent functional-morphologic complex. They may therefore be considered aspects of a single feature, but each nevertheless serves to distinguish *G. larsoni*.

I do not propose to construct a formal phylogeny of *Gregorymys* or attempt to place *G. larsoni* within such a phylogeny at this time. The lack of detailed population studies, the poor stratigraphic control for many of the published specimens, and the abundance of unpublished material prevent an understanding of the interspecific relationships within the genus. In fact, the genus needs a revision. It has not been extensively studied since it was described in 1936 and several species evidently referable to the genus remain to be described (*e. g.*, Robinson, 1968:195). The only population of *Gregorymys* which has ever been studied consists of 15 specimens assigned to *G. formosus* by Macdonald (1970). This sample shows very great dimensional variation in tooth measurements and no statistical treatment was attempted, presumably because the sample was so small and variable, so that it does not provide an understanding of potential ranges in size or morphologic characters within *Gregorymys'* populations. Large samples of *Gregorymys* are evidently available for study (*e. g.*, Macdonald, 1972:30), but such studies have not been undertaken.

Storer (1975:105) suggests that *Gregorymys* may be ancestral to *Lignimus*, a dominantly Clarendonian genus. Transitional forms which might support this relationship have not been reported, but it is at least clear that *G. larsoni* has nothing to do with a *Gregorymys*-*Lignimus* morphocline. *G. larsoni* may be characterized as a persistent survivor of the Arikareean *Gregorymys* morphotype.

AGE AND CORRELATION

The Derby Peak fauna containing *Gregorymys larsoni* has not been studied in detail. It consists of Equidae, Rhinocerotidae, Camelidae, Antilocapridae, and *Mylagaulus laevis* (Larson, 1968; P. Robinson, personal communication). These taxa are not particularly useful for correlation purposes, but the presence of antilocaprids and *Mylagaulus* precludes an age earlier than Hemingfordian. Morris Skinner of the American Museum of Natural History has examined a horse mandible from Derby Peak (UCM 29747) and considers it most similar to specimens from the Lower Snake Creek fauna of Nebraska. Based upon the stage of evolution of this horse, he believes the Derby Peak fauna to be approximately 13.5 m.y. old (personal communication).

K-Ar ages have been determined for many of the volcanic rocks interbedded with vertebrate-bearing sediments in the area surrounding Derby Peak (Larson, 1968; Larson *et al.*, 1975). An age of 10.3 ± .5 m.y. was obtained from the flow immediately above the unit containing the Derby Peak fauna. No rocks below the vertebrate locality on Derby Peak itself have been dated, but flows immediately underlying and interbedded with similar sediments containing poorly preserved vertebrate remains on "W" Mountain and Trapper's Peak nearby have produced dates. Their ages range from 12.4 ± .5 m.y. to 13.4 ± .5 m.y. These ages indicate that the Derby Peak fauna lived between 13 and 10 million years ago.

This faunal and radiometric age evidence strongly suggests that the Derby Peak fauna is equivalent to late Barstovian or early Clarendonian faunas in age (Evernden *et al.*, 1964; Lindsay, 1972). *Gregorymys* has previously been reported only from late Arikareean and early Hemingfordian deposits. A single "entoptychine" tooth has been reported from sediments as young as Clarendonian or Hemphillian in Wyoming (Love, 1961:35), but the data are insufficient to evaluate this occurrence. The species with the closest apparent relationship to *G. larsoni*, *G. riggsi*, is known only from "Arikaree Beds" of Wyoming. Therefore, *G. larsoni* is anomalous in stage of evolution and the possibility that the specimen was redeposited from older sediments must be considered. There are older fossiliferous sediments in the area of Derby Peak. These are the Group 1 rocks of Larson *et al.* (1975), which range in age from 24 to 20 m. y. This age would be consistent with the stage of evolution of *G. larsoni* and a number of unstudied specimens of *Gregorymys* have been collected from deposits of this age east of Derby Peak (Robinson, 1968). However, there is no evidence that the specimen of *G. larsoni* was redeposited. It shows the same type of preservation and does not seem to be more abraded than the other specimens from Derby Peak, which all were apparently transported prior to deposition.

BIOGEOGRAPHY

The *Gregorymys* lineage, based upon its previously recorded occurrences, appeared to have become extinct by middle Hemingfordian time, approximately 18 million years ago. Its presence in the Derby Peak fauna is unexpected. Persistence of a primitive morphological type such as *G. larsoni* could occur through isolating mechanisms which protect it from competition. Topographic isolation in a high-altitude mountain basin may be suggested as such a mechanism in this case, but the geologic evidence for isolation of this kind is not strong. The existence of isolated early Miocene depositional basins in northwestern Colorado is well documented, but the period of volcanism during which the Derby Peak sediments were deposited seems to have been characterized by widespread steppes which connected previously isolated basins and were inhabited by a uniform biota (Izett, 1975; Larson *et al.*, 1975; earlier work cited therein). The widespread tectonism which resulted in the present intermontane basins of northwestern Colorado did not begin until nine or ten million years ago. However, the White River Plateau, of which Derby Peak is presently an outlier, has been a positive structural and topographic feature since its origin in the late Cretaceous. Kucera's (1968) studies show that it was shedding sediments into the basins to the north during deposition of the Derby Peak sediments. Furthermore, his observations on the depositional characteristics of the basalt flows in the Derby Peak area indicate that many of the flows are very localized. It is therefore possible that *Gregorymys larsoni* could have inhabited one or several very small intermontane basins where it was effectively isolated from competitors.

It is interesting to note that Robinson (1968) has observed speciation of early Miocene entoptychines in the area east of Derby Peak which was apparently at least partially controlled by the same isolated intermontane basin type of topography suggested above. If a population of the type mentioned by Robinson became isolated in a high valley on the slopes of the White River Plateau, and if that valley provided a refugium while the lower basins to the east gradually fused, bringing their previously isolated entoptychines and other later-evolved rodents into competition with one another, the population remaining in the high valley might well develop into the sort of taxonomic compromise represented by *G. larsoni*.

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FIRST RECORD OF *TELEOCERAS* (RHINOCEROTIDAE) FROM THE RINGOLD FORMATION, PLIOCENE OF WASHINGTON

by

ERIC PAUL GUSTAFSON[1]

ABSTRACT

The first identifiable vertebrate specimen from the conglomerate middle member of the Ringold Formation, Franklin County, Washington, is a mandible of the short-legged rhinocerotid *Teleoceras*. The middle member of the Ringold had been considered Blancan (Pliocene) in age because of the presence of the early Blancan White Bluffs local fauna in immediately overlying beds. The *Teleoceras* mandible is younger than basalts dated at 8.6 million years. It is similar to *Teleoceras* specimens from the Hemphillian McKay Reservoir local fauna of Oregon, and is probably late Hemphillian in age.

INTRODUCTION

In late December 1974 a partial adult lower jaw with dentition of one side present of the short-legged rhinocerotid *Teleoceras* was found in the very sparsely fossiliferous conglomerate middle member of the Ringold Formation.

Vertebrate fossil faunas from the State of Washington range in age from Arikareean (early Miocene) through Pleistocene, but none of the known faunas has been thoroughly described. The Blancan White Bluffs local fauna of the Ringold Formation, in the Pasco Basin near the center of the Columbia Plateau, has been most recently listed and partly described (Fry and Gustafson, 1974). The specimen described here suggests a change is necessary in the interpreted age for part of the Ringold section, and it indicates that a fauna of Hemphillian age is present in central Washington.

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LOCATION AND DESCRIPTION

The *Teleoceras* mandible (WSM 52685, in the Thomas Burke Memorial Washington State Museum, Seattle) is from about 22 meters (70 feet) below the top of a unit which I (unpublished thesis, 1973) have informally named the Taylor Flat conglomerate (equivalent to the "middle Ringold" of Newcomb, 1958). The exposure (WSM locality C71) is a road cut in section 25, R 28 E, T 11 N, Franklin County, Washington, and in fact the specimen was first seen through a car window.

The specimen compares favorably in most characters with mature specimens of *T. fossiger* (illustrated in Matthew, 1932), though it is smaller than most described specimens of *Teleoceras*. An erroneous preliminary identification (*"Aphelops"*) was published in an abstract (Gustafson, 1976) but the correction was made by the time of the presentation of that paper in April, 1976. The short anterior mandible, with only two premolars present, as well as the rounded ventral margin and anterad-leaning coronoid process, are sufficient characters for the generic identification. Species-level identification is not considered advisable because of the lack of revision of the several described and rather similar species. The dentition is partly abnormal. The third premolar leans anterad at an awkward angle, and the fourth premolar is elevated anteriorly. Apparently the upper premolars which should have occluded with these teeth were broken or absent.

DISCUSSION

The species of the genus *Teleoceras* were listed by Tanner (1975). The earliest occurrence listed is an unnamed species from the early Clarendonian Burge Member of the Valentine Formation in South Dakota, and the latest occurrence is *T. schultzi* in the late Hemphillian Kimball Formation, Nebraska. I have here used the North American Land Mammal Ages as given by Wood et al. (1941) rather than the terms Valentinian (in part = early Clarendonian) and Kimballian (= late Hemphillian) as used by Tanner. Tanner noted that *Teleoceras* evolved from a relatively small animal to a large robust form. However, he mentions that "a smaller tribe of *Teleoceras* may have lived at the same time as *T. schultzi*."

The specimen described here (WSM 52685) appears to be conspecific with undescribed specimens of *Teleoceras* from Hemphillian localities in northern Oregon, particularly Westend Blowout and McKay Reservoir (Shotwell, 1956, 1958). It is considerably smaller than *T. schultzi* and *T. hicksi* and is slightly smaller than *T. fossiger*, though the significance of these size differences remains to be demonstrated. It is near the size of *T. major* Hatcher, and late Clarendonian type species of the genus. It may also be near the size of Tanner's "smaller tribe" from the late Hemphillian of the Great Plains. From these data it appears that the small size of WSM 52685 has in itself little or no time significance.

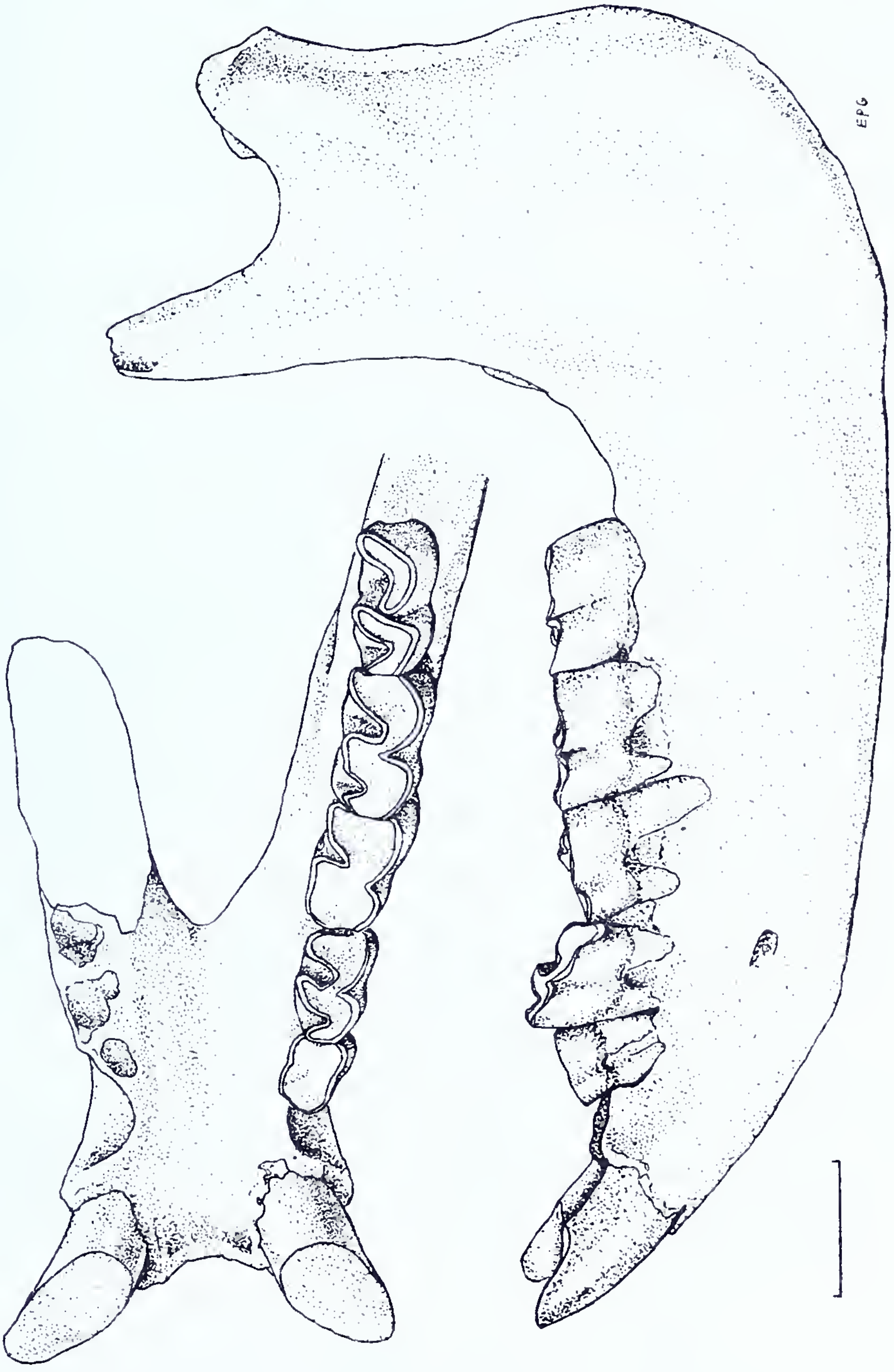

Figure 1. WSM 52685, *Teleoceras* sp. mandible from Taylor Flat conglomerate of Ringold Formation, locality WSM C71, Franklin County, Washington. Occlusal and left lateral views. Scale line equals 5 centimeters.

The Taylor Flat conglomerate, from which this specimen came, is overlain by a 150 meter (500 foot) thick fluviatile section containing an early Blancan fauna (Fry and Gustafson, 1974). No specimens of any rhinocerotid have been recognized from the latter (White Bluffs local fauna of Tedford and Gustafson, 1977), although many hundreds of specimens are known. The Taylor Flat conglomerate is underlain by further sediments (about 60 meters or 200 feet at WSM-C71) and by basalt flows of the Yakima Basalt. The youngest of these are the Ice Harbor flows, which have been dated at 8.6± 0.3 million years using whole-rock K/Ar methods (Swanson and Wright, 1976). With the present data, I consider the Taylor Flat conglomerate probably equivalent in age to deposits overlying the Yakima Basalt in northern Oregon which contain late Hemphillian faunas.

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STUDIES ON FOSSIL PHYLLODONT FISHES: A NEW SPECIES OF *PHYLLODUS* (ELOPIFORMES, ALBULOIDEA) FROM THE LATE CRETACEOUS OF MONTANA

by

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ABSTRACT

Phyllodus paulkatoi, n. sp., from the Late Cretaceous Hell Creek Formation of Montana, is the first Cretaceous record and most primitive member of the genus, lacking the transverse widening of the central row of teeth on the basibranchial tooth plate. A cladistic arrangement of the Phyllodontinae suggests that phyllodontids are derived from albulids through the Early Cretaceous albulid *Casierius*. Phyllodontids represent a poorly-known but common group of albuloid fishes known only from oral tooth plates; the group was distributed along a shallow water "track" extending from epicontinental seas on the North American continent across the North Atlantic to Europe, apparently becoming extinct shortly after separation of Europe and North America in the Early Eocene.

INTRODUCTION

Occurrences of tooth plates of fishes with multiple superposed sets of replacement teeth (phyllodont) have been discussed recently by Estes 1969a, 1969b. This condition has been found in at least seven teleost families but most occurrences in the early Tertiary are referable to the family Phyllodontidae, related to the living albuloid bonefishes or ladyfishes. Two subfamilies Phyllodontinae and Paralbulinae have been named, of which the latter is the more primitive in having greater number of teeth, teeth alternating or irregular rather than directly stacked, and in having hemispherical rather than flattened teeth.

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The two subfamilies are known principally from Paleocene and Eocene localities in North America, Europe, and Africa, and come from sands and clays associated with continental margin deposits or epicontinental seas. The earliest records of the group to date are Campanian and Maastrichtian occurrences of Paralbulinae in North America and Africa.

A recently discovered specimen from the Hell Creek Formation (Maastrichtian) of Montana is of interest because it is the first Cretaceous record of the Phyllodontinae and because it represents what appears to be a primitive species of the genus *Phyllodus*.

SYSTEMATICS

Infraclass Teleostei

Superorder Elopomorpha

Order Elopiformes

Suborder Albuloidei

Family Phyllodontidae

Phyllodus paulkatoi n. sp.

Text Figs. 1-2

Etymology: Named for Paul Kato, a high school student in Glendive, Montana ,who collected the specimen and kindly donated it to the Museum of Paleontology, University of California.

Holotype: University of California, Berkeley, Museum of Paleontology, UCMP 119563, posterior portion of basibranchial tooth plate.

Referred specimens: No other topotypic specimens are known, but Museum of Comparative Zoology, Harvard University 9275-9277, fragments of tooth plates from the Tullock Formation, early Paleocene (Puercan) of Montana, are probably referable to this species. These specimens were previously referred to *Phyllodus toliapicus* by Estes (1969a).

Type locality: UCMP locality V78043, SW 1/4 Sec. 33, T. 16 N, R. 56 E, Dawson County, Montana. Soft olive sandstone in base of badland bluffs approximately 3/4 mile South from Highway I-94, five miles east of Glendive, Montana.

Horizon: Hell Creek Formation, probably not far below the basal ("Z") coal bed.

Age: Late Cretaceous (Maastrichtian).

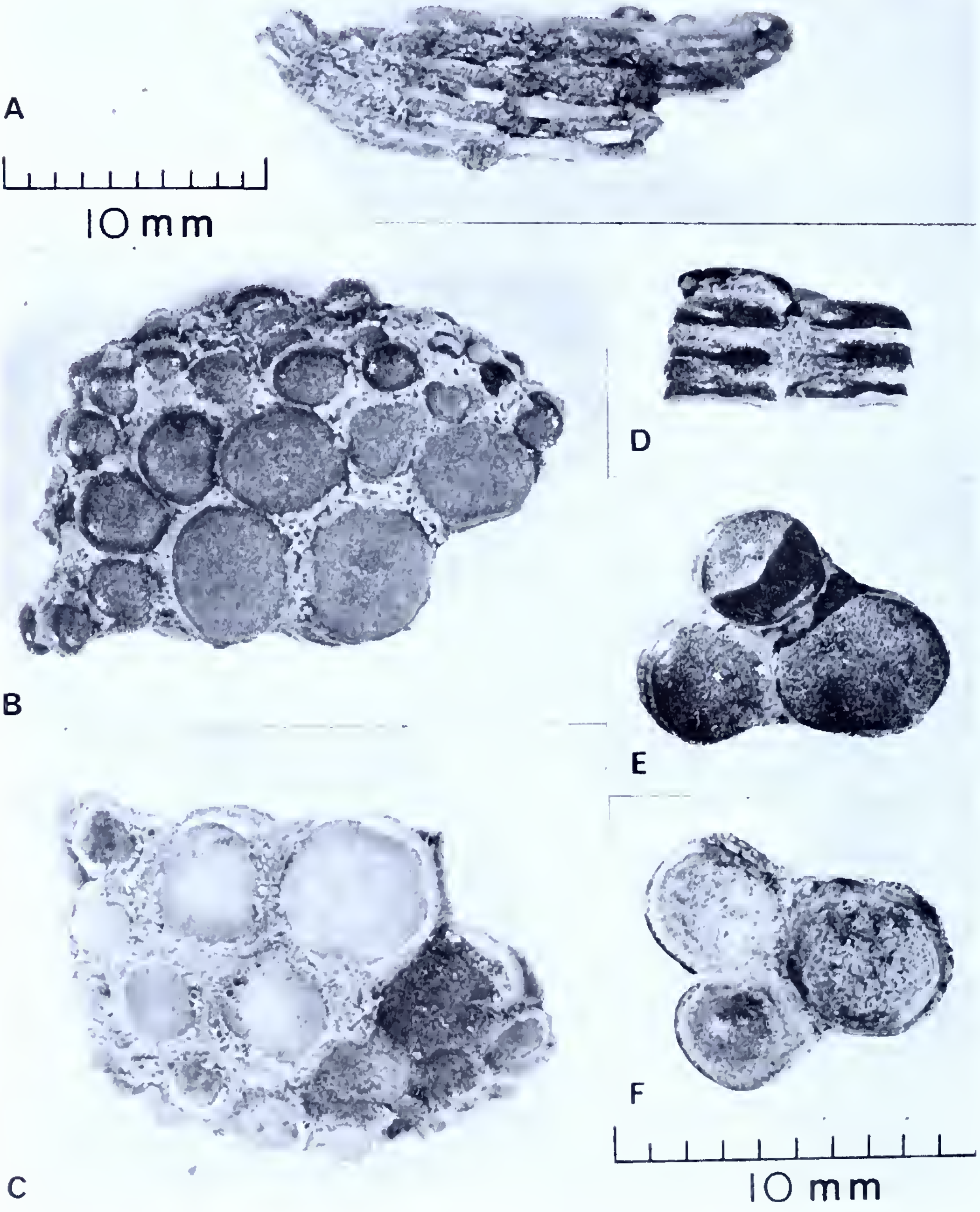

Figure 1. *Phyllodus paulkatoi*, n. sp.: A, lateral; B, occlusal and C, basal views of type specimen, UCMP 119563, basibranchial tooth plate; Upper Cretaceous (Maastrichtian), Hell Creek Formation, Glendive, Montana. D, lateral; E, occlusal and F, basal views of referred specimen, MCZ 9277, Lower Paleocene (Puercan), Purgatory Hill, McCone County, Montana.

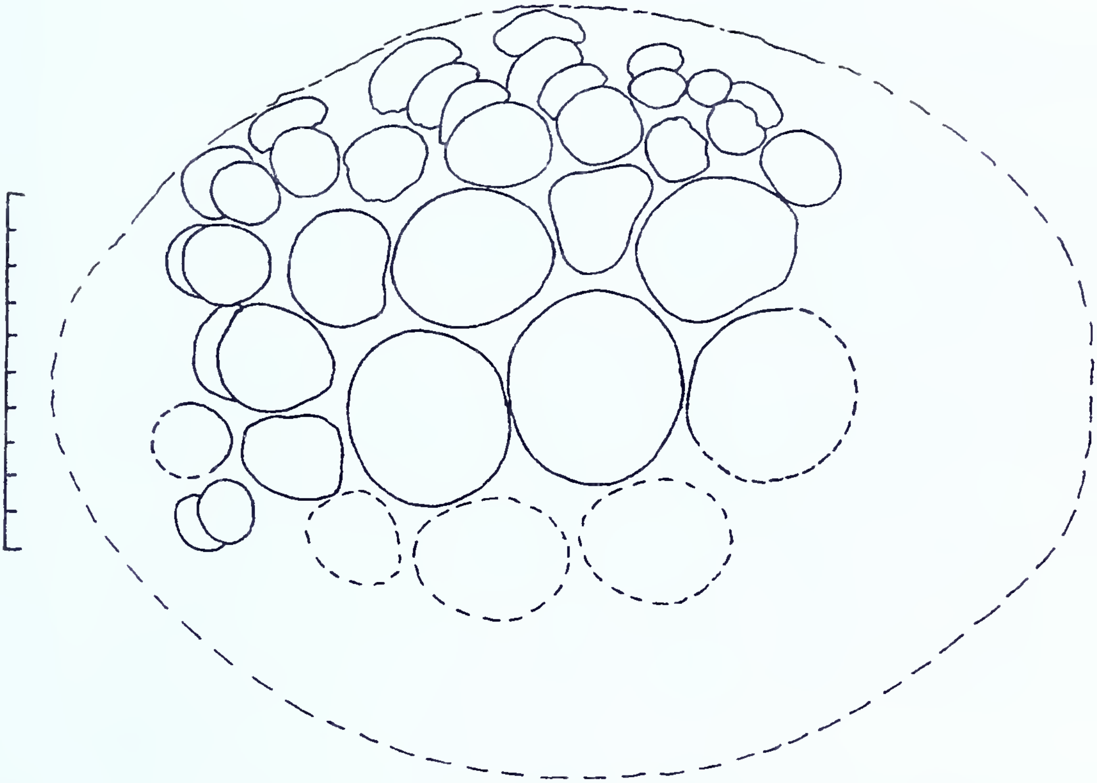

Figure 2. *Phyllodus paulkatoi*, n. sp.; type specimen, UCMP 119563, Upper Cretaceous (Maastrichtian), Hell Creek Formation, Glendive, Montana. Restoration of basibranchial tooth plate.

Diagnosis: Differs from *Phyllodus toliapicus* and *P. centralis* in having a central longitudinal row of three slightly enlarged suboval teeth; differs from *P. toliapicus* in having suboval rather than transversely-elongated teeth in the central row; sculpture of tooth crowns slightly coarser than those of the above species.

Description: Teeth subcircular or suboval; tooth crowns finely rugose when unworn; tooth diameter range 1.4 - 4.5 mm; replacement teeth usually stacked in regular columns below functional teeth; teeth flattened, cavity not apparent; interstitial bony matrix little or absent. Central row of three teeth very little enlarged (diameters 5.0 - 5.4 mm) surrounded by row of somewhat smaller teeth (diameters 3.0 - 4.6 mm), at least two peripheral rows of teeth 1.4 - 3.0 mm in diameter.

In thin section the teeth consist of a basal layer of orthodentine and a thinner crown layer of modified dentine. The type appears to lack (in the one thin section made) the few prominent medullary canals seen in the Tullock Formation specimens, and there is no tendency to develop groupings of the orthodentinal tubules at the pupal surface that are seen in other phyllodontines; in this respect the type specimen is more like the paralbulines. These preliminary observations, however, may be more the result of regional limitation of these structures and the single section made. An analysis of phyllodontid tooth histology is being made by Mr. Floyd Richey and more definite statements must await completion of his study.

Discussion: Degree of enlargement of central teeth in *Phyllodus* varies extensively as shown in large Eocene samples from the London Clay (England) and Aquia Formation (Maryland) but no known specimens of *P. toliapicus* have suboval teeth in the central row of three or four teeth; some degree of transverse elongation always occurs. Casier (1967) named *P. centralis* based on two late Paleocene specimens from Belgium in which the central tooth is a single enlarged one rather than a row of three. Lack of transverse elongation of the central teeth in the Hell Creek specimen along with the somewhat more coarse tooth crown sculpture seems to justify a new species, however, more primitive in this respect than the other two species.

Estes (1969a) commented on fragmentary early Paleocene specimens of *Phyllodus* from the Tullock Formation of Montana, referring them to *P. toliapicus* but noting possible future reference to a new species. *P. paulkatoi* and the Tullock Formation specimens both have a coarser sculpture pattern than other *Phyllodus*. In addition, lack of elongated central teeth in *P. paulkatoi* suggests that their absence in the Tullock specimens could have been real rather than simply the result of an incomplete record, and the Tullock specimen figured by Estes (1969a, Fig. 1a-c), while slightly smaller than the type of *P. paulkatoi*, appears to represent one of the slightly enlarged row flanked by two teeth of the lateral row (Figure 1b). Thus at least provisionally, the Tullock specimens can be referred now to *P. paulkatoi*, giving a range for the latter of Maastrichtian-Puercan (Montian equivalent); *P. toliapicus* thus is first known from the late Paleocene of Europe and Africa.

Geological occurrence: The unique specimen of *Phyllodus paulkatoi* was found in the very fossiliferous bank of a dry creek bed, associated with osteichthyan, reptilian and mammalian fossils including a 10 cm dinosaurian centrum. Careful prospecting in the immediate vicinity disclosed a fragment of *Triceratops* jaw and the well-preserved fragments of two teeth of *Tyrannosaurus rex*. The basal or "Z" coal seam is well exposed about 3/4 mile away, near Highway I-94; this bed is widely used as a "formula" separator between Cretaceous and Paleocene beds (Brown 1962) but the relationship between the bed from which the specimen of *P. paulkatoi* came and the "Z" coal bed is difficult to determine in this area. The closely

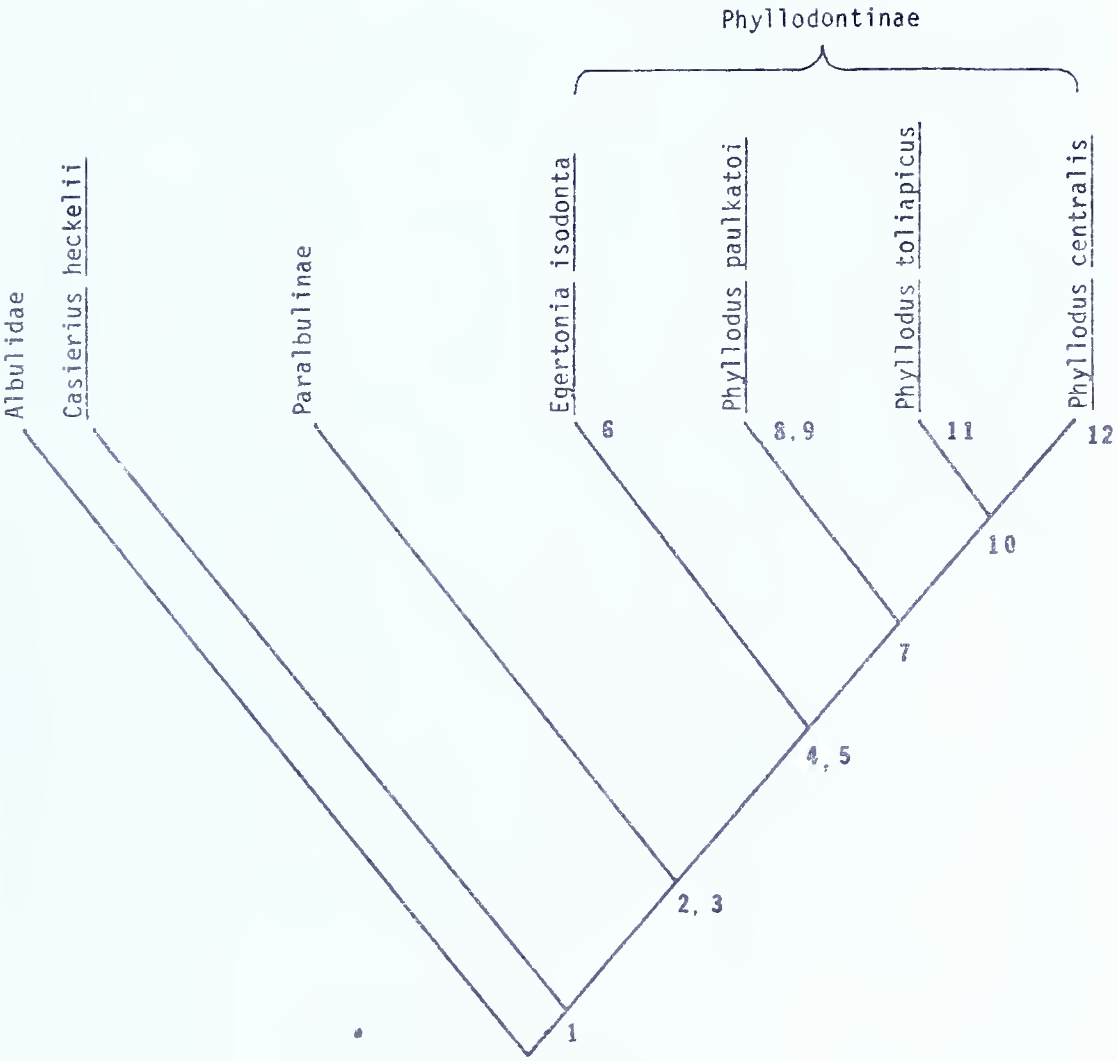

Figure 3. Cladogram expressing presumed relationships among members of the subfamily Phyllodontinae and its relationship to Paralbulinae and Albulidae. Numbers refer to shared-derived characters discussed in the text.

associated dinosaurian remains seem, however, to confirm the Cretaceous age of the specimen.

Affinities of the Phyllodontinae: The primitive morphology of *Phyllodus paulkatoi* provides an opportunity to re-evaluate the relationships of the species presently included in the subfamily Phyllodontinae. The most common species of *Phyllodus* is *P. toliapicus*, known from many Late Paleocene and Early Eocene localities in Europe, and Early Eocene in North America. *P. centralis*, if it is a species rather than simply an occasional variant of *P. toliapicus*, is known only from the Late Paleocene and Early Eocene of Europe if *"Diaphyodus" ovalis* is referable to *P. centralis* as suggested by Estes (1969a). Dr. Peter Wellnhofer (in litt. 1978) notes that the type of *"D." ovalis* has been lost, and that the age of the deposits from which it came is Early Eocene rather than Late Eocene as in Estes (1969b). The cladogram in Figure 3 shows a possible arrangement of these three species and their presumed morphological ancestor *Egertonia isodonta*, a rare species known from Late Paleocene through Middle Eocene of Europe and Middle Eocene of Barbados. When placed on a geochronologic scale (Fig.4) the only problem arising with the cladistic arrangement is the late occurrence of *E. isodonta*, but it is a rare species and clearly more primitive than species of *Phyllodus*; perhaps it will eventually be found to occur in the Cretaceous. These species, which together constitute the Phyllodontinae, appear to be related to the Paralbulinae on the basis of the shared-derived character states of (2) loss of pterygoid tooth plates, a loss parallel to loss of pterygoid plates in Division III fishes; Greenwood et al. (1966), and (3) suboval shape of tooth plates, both of which states separate these groups from their presumed ancestral group, the Albulidae. Relationship to the albulids was discussed by Estes (1969a) and rests in great part on similarity of basibranchial and skull bone impressions on these tooth plates. These similarities are convincingly close but there is still little similar data available for related groups. A possible intermediate between albulids and phyllodontids is *Casierius* (Estes, 1969b), from the Early Cretaceous of North America and Europe, which appears to be albulid in having elongated tooth plates and the retention of pterygoid plates; it is, however, a phyllodont form. *Casierius* and the phyllodontids may be paraphyletic groups but there is insufficient information at present on which to base such a decision; for the present they are considered to be related and thus the phyllodont condition (1) is used to link them although they are placed in separate families here. Resolution of the relationships of phyllodontids and albulids must await associated skeletons and tooth plates.

Regardless of these problems of ancestral relationships, the species included in the Phyllodontinae seem to form a closely-knit group. All included species share the derived states of (4) flattened teeth that are (5) regularly stacked in columnar piles. *Egertonia isodonta* is the most primitive of the group in having subequal teeth

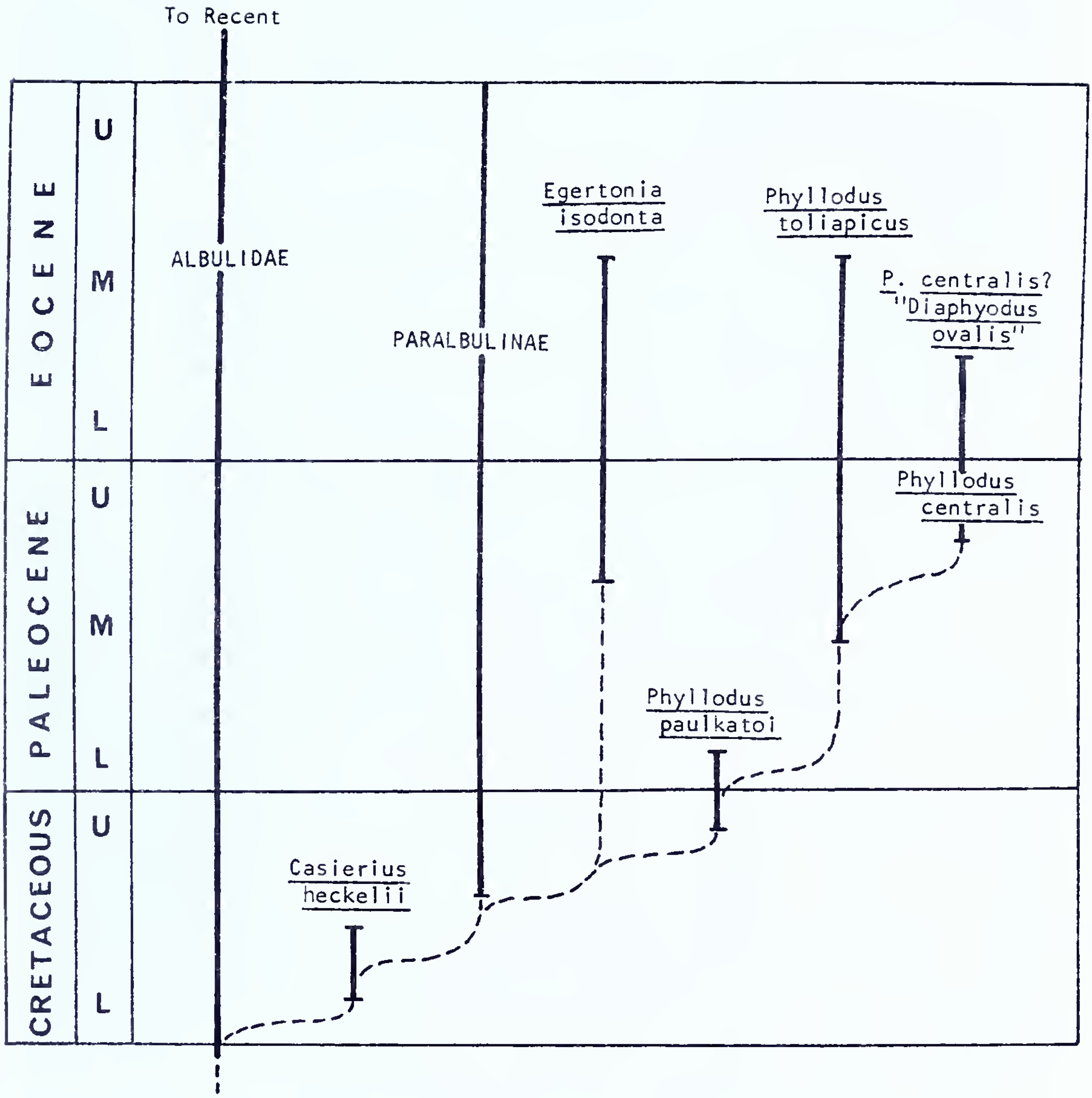

Figure 4. Stratigraphic and presumed phylogenetic relationships of Phyllodontidae and their immediate ancestors. Vertical bars indicate the stratigraphic range of each taxon; dotted lines express relationships.

and its only unique feature is (6) a sparse, punctate sculpture. *Phyllodus* is derived on the basis of (7) a tendency to enlarge the central row of three or four teeth. *Phyllodus paulkatoi* has (8) a well-developed, fine granular sculpture and (9) the central row of teeth is slightly enlarged but they are not elongated. Both *P. toliapicus* and *P. centralis* share (10) a very fine, microgranular sculpture; the former has (11) the central row of 3 or 4 teeth transversely widened, the latter has (12) only a single relatively enormous tooth in the central row.

Paralbulines, which are not otherwise discussed here, differ from phyllodontines in having a much greater degree of interstitial matrix between teeth, having irregularly-stacked teeth and domed surfaces of the basibranchial tooth plate that meet a concavity in the parasphenoid plate. The adaptation for crushing was thus of a slightly different form from that of phyllodontines, which have flatter occlusal surfaces of the tooth plates.

Biogeography of the phyllodontids: Estes (1969a) suggested origin of the Phyllodontidae in shallow epicontinental North American seas. More recent plate tectonic analysis of the North Atlantic region (See McKenna, 1975) emphasizes the closeness of North America and Europe in the Cretaceous and the lack of a Northern Atlantic connection to cold Arctic waters. Many species of fishes developed in this early North Atlantic region and became widely distributed in Cretaceous and Early Cenozoic times. The shallow-water habitats in which phyllodontids occur from Late Cretaceous through Eocene time were widespread on the borders of the North Atlantic and the related shallow epicontinental seas on the North American continent.

Casierius gaultinus, if it is actually an ancestral group to phyllodontids, had a similar, broad distribution in Early Cretaceous seas of this same region, as it is known in Texas, England and Italy. It is thus likely, given the known distribution pattern of *Casierius* and phyllodontids, that no center of origin existed for the group, which occupied what Croizat, Nelson and Rosen (1974) have called a "generalized track", with coincident distributions of a number of other fish groups (See e.g., Leriche, 1942). *Phyllodus paulkatoi*, representing an early stage in phyllodontine evolution, was probably distributed widely in this shallow-water "track" (of which we still have insufficient Late Cretaceous and Paleocene records in Europe). The Tullock Formation record (if correctly assigned) would have probably been from land-locked populations (Love, McGrew and Thomas, 1963) but oceanic populations gave rise to the later *P. toliapicus* which itself ranged widely over this "track". Phyllodontine evolution thus can be explained more reasonably in terms of vicariance biogeography than in terms of a center of origin.

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